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LIMB OWNERSHIP AND VOLUNTARY ACTION: HUMAN BEHAVIORAL AND NEUROIMAGING STUDIES

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THESIS FOR DOCTORAL DEGREE (Ph.D.)

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ABSTRACT

To be able to interact with our surroundings in a goal directed manner, we need to have sense what our body is made up of as well as a sense of being able to control our body. These two experiences, the sense of body ownership and the sense of agency, respectively, are fundamental to our self-perception but have historically not received any notable attention from the scientific community. This lack of interest probably stems from the fact that these experiences are phenomenologically thin in our everyday lives and that we cannot voluntarily turn them off, they are constantly there. However, for patients suffering from disturbances in the processes underlying these experiences, their importance becomes exceedingly clear. Lesions in the frontal, temporal or parietal lobe can lead to patients losing the sense of ownership of their limb (asomatognosia), and sometimes even attributing the limb to someone else (somatoparaphrenia). Similarly, patients suffering from lesions in the frontal lobe, parietal lobe or corpus callosum can experience a lack of control over their own hand (anarchic hand syndrome), while patients suffering from schizophrenia display difficulties in distinguishing self-generated from externally generated actions, implicating disturbances in the processes underlying the sense of agency.

With the discovery of body illusions, combined with functional neuroimaging, it became possible to study the perceptual and neural mechanisms of the sense of body ownership in healthy volunteers. Studies using these illusions have elucidated the perceptual rules of body ownership as well as its neural correlates and has given rise to a number of different philosophical, neurocognitive and computational models of the sense of body ownership. Meanwhile, the sense of agency has mostly been studied disconnected from the sense of body ownership, focusing on agency over self-generated external sensory effects such as auditory tones. This thesis sought to bring these two experiences together and advance our knowledge of the perceptual and neural mechanisms underlying the sense of body ownership and the sense of agency as well how these two experiences interact. **Studies I & II** investigate certain aspects of the sense of body ownership, and in particular its relation to the visuo-proprioceptive recalibration of limb position often seen in bodily illusions. **Study III** investigated how this visuo-proprioceptive recalibration is related to voluntary, but unconscious movements. **Study IV** investigated the neural correlates of the sense of body ownership and agency as well as their interaction.

In **Study I**, we present empirical evidence in favor of models where the subjective sense of limb ownership is not reliant on a visuo-proprioceptive recalibration of perceived limb position. In **Study II**, we show that the subjective sense of limb ownership and the visuo-proprioceptive recalibration of limb position have similar temporal decay curves, suggestive of a causal relationship between them. In **Study III**, we show that the increase in the recalibration of limb position seen in active movements is not dependent on conscious intention, action awareness or salient error signals, indicative of an unconscious efference copy-based mechanism. Finally, in **Study IV**, we identify brain regions in the frontal and parietal lobe which are associated with the sense of body ownership, while brain regions in the frontal and temporal lobe are associated with the sense of agency. We show that the sense of agency in the presence of a sense of body ownership (i.e., agency of bodily actions) is associated with increased activity in the primary sensory cortex, whereas the sense of agency in the absence of ownership (i.e., agency of external events) is associated with increased activity in the visual association cortex. Together, these findings shed light on the perceptual and neural mechanisms underlying the sense of body ownership and agency as well as their interaction.

LIST OF SCIENTIFIC PAPERS

I. **Abdulkarim** & Ehrsson (2016). No causal link between changes in hand position sense and feeling of limb ownership in the rubber hand illusion. *Attention, Perception & Psychophysics.*

II. **Abdulkarim** & Ehrsson (2018). Recalibration of hand position sense during unconscious active and passive movements. *Experimental Brain Research.*

III. **Abdulkarim**, Hayatou, Ehrsson (2020). Sustained rubber hand illusion after end of visuo-tactile stimulation with similar time courses for reduction of subjective ownership and proprioceptive drift. *Manuscript.*

IV. **Abdulkarim,** Guterstam, Hayatou, Ehrsson (2020). The neural substrates of body ownership and agency and their interaction during voluntary movement. *Manuscript.*

LIST OF ADDITIONAL PUBLICATIONS

Guterstam, **Abdulkarim**, Ehrsson (2015). Illusory ownership of an invisible body reduces autonomic and subjective social anxiety responses. *Scientific Reports.*

Gentile, Björnsdotter, Petkova, **Abdulkarim**, Ehrsson (2015). Patterns of neural activity in the ventral premotor cortex reflect a whole-body multisensory percept. *Neuroimage.*

CONTENTS

LIST OF ABBREVIATIONS

RF	receptive field
fMRI	functional magnetic resonance imaging
EEG	electroencephalography
ECoG	electrocorticography
EMG	electromyography
TMS	transcranial magnetic stimulation
BOLD	blood oxygen level dependent
FWHM	full-width-at-half-maximum
GLM	general linear model
ROI	region of interest
SMA	supplementary motor area
pre-SMA	pre-supplementary motor area
PMv/PMd	ventral (v) and dorsal (d) premotor cortex
IPS	intraparietal sulcus
PPC	posterior parietal cortex
SMG	supramarginal gyrus
STG	superior temporal gyrus
DLPFC	dorsolateral prefrontal cortex

1 INTRODUCTION

1.1 THE PHYSICAL BODY

There are primarily two ways in which we as humans interact with the outside world (outside the boundaries of the physical body). Through the microscopic transport of ions, atoms and molecules across cell membranes, we absorb nutrients, exchange gases, excrete waste etc., whereas through macroscopic movements, for which the executant is skeletal muscle, we relocate our body and our limbs in space. The former is outside the realm of volition, we cannot control the movement of elementary particles by will, whereas the latter is intimately linked to volition. To move our body and relocate our limbs in space in a goal directed manner, we need to have a sense of what belongs to our body and not, since it would be fruitless to attempt to move bodies or limbs that do not belong to us by sheer will. This sense of owning one's body has, despite the fact that our physical body is the vessel through which we both observe and interact with our surroundings, received little attention from the scientific community. The lack of interest in this so-called body ownership probably stems from difficulties related to the fact that the feeling of owning one's body cannot be voluntarily turned off, it is constantly there and we experience, as the psychologist William James so elegantly expressed it, "the same old body, always there" (James, 1890). The physical body is indeed a peculiar object in the world, aside from the fact that it likely is the most familiar object to us, we experience it from the "inside", where sensory information from our exteroceptive, as well as interoceptive senses are all experienced from inside our bodies. With that said, the experience of one's own body contains more than the sense of ownership, it also includes for instance the sense of agency (controlling the body) and the sense of self-location (locating the body in space). This thesis aims at elucidating the perceptual and neural mechanisms of two of these basic aspects: the sense of body ownership and the sense of agency.

1.2 THE SENSE OF BODY OWNERSHIP

1.2.1 Bodily illusions

The study of the sense of body ownership was until recently confined to case studies of patients with disturbances in the perception of their own bodies. These studies were limited by both the small number of patients displaying such disturbances, but also by the fact that the underlying pathologies displayed a staggering diversity, ranging from brain lesions to amputations. However, with the development of body illusions, it became possible to study the sense of body ownership in a controlled laboratory setting in healthy volunteers. In 1998, psychologists Matthew Botvinick and Jonathan Cohen published the seminal paper on the so-called rubber

hand illusion (Botvinick & Cohen, 1998). By stroking a humanoid rubber hand placed in view of the participants and the participants' real hand (which was hidden from sight), synchronously and at corresponding places, the participants would start to feel the touches of the brush on the rubber hand and further that the rubber hand was their hand. Since its publication, the range of body illusions have extended to include whole bodies (Petkova & Ehrsson, 2008), invisible body parts (Guterstam et al., 2013) and invisible bodies (Guterstam et al., 2015). Moreover, the perceptual rules guiding these bodily illusions have been elucidated, these include: the spatial rule(s) (i), the temporal rule (ii), the anatomical rule (iii) and the tactile congruence rule (iv), which I will exemplify below in the case of the rubber hand illusion. The spatial rule(s) (i) postulate that in order to perceive the rubber hand as one's own, the visuo-tactile stimuli need to be spatially congruent (e.g., by stroking the participant's hand and the rubber hand at corresponding places) (Costantini & Haggard, 2007; Gentile et al., 2013; Guterstam et al., 2013), the viewed hand needs to be within a certain distance of the felt hand (approximately 27,5 cm, (Kalckert & Ehrsson, 2014b; Lloyd, 2007)) and the touches need to be applied in the same direction with regards to a hand-centered spatial reference frame (Costantini & Haggard, 2007). The temporal rule (ii) postulates that the visuo-tactile stimuli have to be temporally synchronous, with the illusory experience declining significantly as delays between the seen and felt touches approach 300 ms (Shimada et al., 2009), and in fact, a frequently used control condition introduces a temporal delay between the seen and felt touches in the range of 500-1000 ms, which has reliably been shown to abolish the illusory sense of body ownership (Abdulkarim & Ehrsson, 2016; Armel & Ramachandran, 2003; H Henrik Ehrsson et al., 2004; Kalckert & Ehrsson, 2014a; Tsakiris & Haggard, 2005). The anatomical rule states that the viewed body parts have to be humanoid in shape, where a block of wood does not induce the illusion (Guterstam et al., 2013; Tsakiris et al., 2010; Tsakiris & Haggard, 2005) and is frequently used as a control condition. One study investigated how much structural similarity to a humanoid hand the object being stroked has to have in order to induce a sense of ownership. The results indicated that the object had to resemble a hand in both shape and structure to induce a sense of body ownership (Tsakiris et al., 2010). On the other hand, the material of the hand seems to matter less, since the rubber hand has been induced with wooden hands (Kalckert & Ehrsson, 2012), metallic hands (Rosén et al., 2009), 3D digital images of hands presented in head-mounted displays (Gentile et al., 2013) and hands with a skin color that differs from that of the participant (Farmer et al., 2012). Finally, the tactile congruence rule (iv) is based on recent studies that have shown that incongruencies between the properties of the tactile stimuli used on the rubber hand and the participants real hand lead to significant reductions of the illusion strength. A reduction was observed for object incongruency (for instance pencil vs

paintbrush) (Ward et al., 2015), whereas no differences were seen for surface incongruency (for instance piece of cotton vs sponge) (Schütz-Bosbach et al., 2009), perhaps reflecting the mismatch tolerance of this rule.

Following the classical rubber hand illusion, several body illusions have been published, including "the invisible hand illusion" where the rubber hand is removed from the setup, and instead the contours of an invisible hand is delineated in empty space leading to an embodiment of that portion of empty space (Guterstam et al., 2013). Similarly, the invisible body illusion made use of head-mounted displays to induce the illusion of owning an entire invisible body by delineating the contours of an invisible body in empty space (Guterstam et al., 2015). Most interestingly, however, the moving rubber hand illusion moved away from purely visuo-tactile stimulation to induce illusory ownership of the rubber hand (Kalckert & Ehrsson, 2012, 2014a). In the moving rubber hand illusion, a wooden or rubber hand with flexible joints is placed on a small table, under which the participant's real hand is hidden. The index finger of the rubber hand and the participant's hand are connected with a rod that passes through a small hole in the table, linking the movements of the participant's hand and the rubber hand. When the participants move their index finger, the index finger of the rubber hand will move in synchrony and with the same amplitude. After a few such tapping movements with the index finger, the participants will start to experience that the rubber hand is their hand, and further that they can control it. What is particularly interesting about the moving rubber hand illusion is that it induces an illusory sense of body ownership as well as a sense of agency over the rubber hand, and even more intriguingly, if the fingers are moved passively, the sense of body ownership is retained whereas the sense of agency is diminished. Conversely, if the rubber hand is placed in an anatomically incongruent position (rotated 180 degrees) and the participants actively move their index finger and thus the index finger of the rubber hand, they will experience a sense of agency over the rubber hand, while no sense of body ownership of the rubber hand will be elicited (Kalckert & Ehrsson, 2012).

There are different ways to measure the sense of body ownership in these bodily illusions. Explicit judgements of the sense of body ownership through questionnaires are widely used to evaluate the existence of body ownership or not (Abdulkarim & Ehrsson, 2016; Botvinick & Cohen, 1998; Kalckert & Ehrsson, 2014a; Longo et al., 2008). However, such explicit judgements can be influenced by cognitive biases, task compliance and suggestibility, and to this end, implicit tasks and measures have also been developed. The so-called skin conductance response measures the changes in galvanic skin conductance in response to threatening stimuli directed at the illusory limb or body (Armel & Ramachandran, 2003; Guterstam et al., 2013, 2015; Petkova & Ehrsson, 2008). The increase in skin conductance in response to such stimuli in conditions with ownership of the illusory body or body part compared to control conditions in which no ownership is present has been interpreted to be due to increased sweating related to an autonomic stress response (Armel & Ramachandran, 2003; H Henrik Ehrsson, 2007; Guterstam et al., 2011). Another implicit measure is the so-called proprioceptive drift, which is the change in perceived limb location before and after the induction of the rubber hand illusion. The proprioceptive drift is measured by removing visual cues of the position of the rubber hand and the participant's real hand, either by occluding them from sight or by having the participants close their eyes and subsequently ask the participants to indicate the perceived location of their limb. In the illusory conditions, the participants will display a larger drift in perceived limb location towards the rubber hand compared to the control conditions. The proprioceptive drift has been widely used as a measure of the illusion, probably due to the fact that it is easy to administer, does not require much in terms of technical equipment, and has been shown to correlate with the illusory experience (Botvinick & Cohen, 1998; Costantini & Haggard, 2007; H. Henrik Ehrsson et al., 2005; Guterstam et al., 2013; Longo et al., 2008; Samad et al., 2015; Tsakiris & Haggard, 2005). However, recent findings have suggested that the proprioceptive drift and the subjective experience of body ownership are dissociable (Abdulkarim & Ehrsson, 2016; Rohde et al., 2011), and therefore in **Study II**, we wanted to investigate the temporal dynamics of the proprioceptive drift and the subjective illusion ratings, in particular we wanted to investigate their rate of reduction following the end of the visuo-tactile stimulation in the rubber hand illusion.

1.2.2 What is the sense of body ownership?

When we look at our hands, we immediately feel that they belong to us. The term "sense of body ownership" refers to this subjective sense (or feeling) that a body part or body belongs to one's self. One hurdle to overcome with studying such subjective experiences is how to

measure them, and to this end, the aforementioned explicit and implicit outcome measures of the sense of body ownership have been developed. Somewhat more challenging than the practical problem of how to measure a subjective experience, the main issue with subjective experiences is to try and understand what they are and why they exist, and accordingly, the philosophical discourse regarding the sense of body ownership have to large extent focused on this problem. Below I will present some philosophical viewpoints on the sense of body ownership before delving into the neuroscientific models of body ownership, and although there is an overlap between these two disciplines, the neuroscientific effort has, in contrast to the philosophical one, focused on elucidating the underlying perceptual and neural mechanisms (the 'how') rather than trying to explain what it is and why it exists (the 'what' and 'why').

A review of the main philosophical viewpoints regarding the sense of body ownership was recently described in a philosophical essay by Fredrique de Vignemont, where she divided them into three main categories – the eliminativist, the irreductionist and the reductionist viewpoints (Frédérique de Vignemont, 2015). The eliminativist view is that there is nothing more than the mere physical properties of the things we experience, in the context of body ownership, there is no feeling of "mineness" and the sense of body ownership is nothing more than knowledge of the fact that one's body belongs to one's self (Bermúdez, 2011). This position is hard to reconcile with the reported experiences of body illusions where the participants report a sense of body ownership over inanimate limbs and bodies despite knowing it cannot be theirs (Botvinick & Cohen, 1998; Guterstam et al., 2011; Petkova & Ehrsson, 2008). The irreductionist viewpoint on the other hand, holds that the there is indeed a feeling of "mineness", and that the sense of ownership of one's body is an irreducible sensation of the body which cannot be described in terms of any other bodily sensations or experiences. This irreductionist position is difficult to contest since it ultimately relies on ruling out every possible reductionist account and hence, I will not discuss it further in this thesis.

The reductionist viewpoint(s) hold that the sense of body ownership can be reduced to other bodily sensations, where some of the most commonly held reductionist positions grounds the sense of body ownership in (i) the affective coloring of events or objects related to the physical body (F de Vignemont, 2017), (ii) the spatial boundaries of the physical body, within which once can have perceptual experiences (Martin, 1995), (iii) the sense of agency over the body (Gallese & Sinigaglia, 2010) and (iv) a multisensory representation of the body (H. Ehrsson, 2012; Henrik H. Ehrsson, 2020; Guterstam, 2016). According position (i), the sense of body ownership is viewed as the affective component of bodily perception, where a distinction between the purely descriptive and affective components of bodily perception is made. In

essence, the account suggests that disturbances in the sense of body ownership such as asomatognosia (failure to recognize body parts as one's own) is the bodily equivalent of Capgras syndrome (Frédérique de Vignemont, 2018), where the patients suffering from Capgras syndrome recognize the physical features of familiar individuals but lack the normal affective reaction to them, subsequently interpreting the individuals as being imposters (Capgras & Reboul-Lachaux, 1994). This affective reaction towards the physical body is proposed to be ultimately aimed at protecting the body from harm. However, this reductionist position of body ownership fails to account for situations in which affective reactions toward physical bodies is unaccompanied by body ownership, for instance a mother carrying her child most likely experience affective reactions toward the body of the child, and likely display a protective behavior if the child's body is threatened, but does not experience any sense of ownership of the child's body.

Position (ii) holds that the sense of ownership is grounded in the spatial boundaries within which one can have sensory experiences (i.e., the borders of the physical body) (Martin, 1995), which seems implausible based on the literature on tool use that show that using tools extend the sense of touch to include the tools (Maravita & Iriki, 2004), as well as extends the space within which visuo-tactile stimuli are integrated (the so-called peri-personal space) (Guterstam et al., 2018). Moreover, this reductionist position is further contradicted by the fact that the sense of ownership does not necessarily correlate with the recalibration of limb position (Holle et al., 2011; Rohde et al., 2011), which one would expect if the sense of body ownership was completely grounded in the spatial position of one's body.

Reductionist position (iii) holds that the feeling of ownership is grounded in the sense of agency (i.e., controlling the body) (Gallese & Sinigaglia, 2010). Intuitively, it seems plausible that the sense of ownership would be grounded in the sense of agency, since the sense of controlling one's body presupposes a sense of said body being one's own. However, this viewpoint also falls on empirical evidence, since the sense of body ownership is maintained during passive movement, while there's no sense of agency and paralyzed patients do not commonly report disturbances in the sense of body ownership, while the sense of agency over the affected body parts is diminished, dissociating the two phenomena. Furthermore, behavioral studies employing body illusions have displayed a perceptual dissociation between the two phenomena, indicating that they are separate experiences (Kalckert & Ehrsson, 2012, 2014a).

Finally, the reductionist position (iv) holds that the sense of body ownership is grounded in a multisensory representation of the body, which is built up and maintained according to principles of multisensory binding and integration (see below). This position draws support

from the neurological literature on patients with disturbances in the sense of body ownership, who often present with lesions in multisensory brain regions (Critchley, 1953; Feinberg et al., 2010; Vallar & Ronchi, 2009), as well as from the neuroscientific literature on body illusions which show that the sense of body ownership obeys multisensory congruence rules (Costantini & Haggard, 2007; Henrik H. Ehrsson, 2020; Gentile et al., 2013; Guterstam et al., 2013; Kalckert & Ehrsson, 2014b; Longo et al., 2008; Shimada et al., 2009) and is associated with activity in multisensory brain regions (H Henrik Ehrsson et al., 2004; H. Henrik Ehrsson et al., 2005; Gentile et al., 2013; Guterstam et al., 2013). The studies in this thesis are to a large extent consistent with this reductionist position (iv) (although the presence of an irreducible component cannot be ruled out) and while being an elegant solutions to the question of what the sense of body ownership is, the remaining question of why it exists is discussed at the end of this thesis.

Parallel to the philosophical discourse, various neuroscientific models of ownership, driven by empirical findings on body illusions and theorized around the integration of visual, tactile and proprioceptive signals have been developed. In the first model of body ownership proposed by Botvinick and Cohen, the sense of body ownership is brought about by tri-modal integration of vision, touch and proprioception (Botvinick & Cohen, 1998); if I see my hand in an anatomical position that is congruent with the proprioceptive signals, while receiving sensory input from the hand, the brain will interpret the hand my own. Furthermore, Botvinick and Cohen state that *"the illusion's spurious reconciliation of visual and tactile inputs relies upon a distortion of position sense"* (p.756), a proposition that is challenged by the fact that the recalibration of hand position sense can happen in the absence of any changes in the subjective sense of body ownership (Holmes et al., 2004, 2006; Makin et al., 2008) and that some rubber hand illusion studies failed to detect any correlation between changes in hand position sense and the sense of body ownership (Holle et al., 2011; Rohde et al., 2011). Tsakiris and colleagues, on the other hand, proposed that the sense of body ownership is brought about by three critical comparisons, the first between the visual features of the viewed body and an internal representation of the physical body, the second between the position of the viewed body and the proprioceptively felt body, and finally between the viewed and felt tactile input (Tsakiris, 2010). However, the fact that ownership of invisible body parts is possible (Guterstam et al., 2013) provide empirical evidence contradicting this model, since the visual input of a hand is missing, and hence the correspondence of the first comparison should decrease. Finally, Makin et al. placed great emphasis on visuo-tactile integration in peri-personal space leading to referral of touch to the viewed body part, which provides positive feedback to existing processes of visuo-proprioceptive recalibration updating the multisensory

representation of the body (Makin et al., 2008). These neurocognitive models, although some are yet to be dismissed by empirical evidence, have to a large degree been replaced by computational models of multisensory integration. The computational models formalize many of the empirically discovered perceptual rules that have been proposed in the neurocognitive models on body ownership while also taking into account sensory and non-sensory prior perceptual experiences and assumptions regarding the relationship of the sensory signals.

1.2.3 Multisensory mechanisms

In our everyday lives, the brain is constantly showered with sensory signals which have to be organized, filtered and (some subsets of the signals) integrated in order to give rise to coherent perceptual experiences. For instance, on my daily walk to work, I hear and see the cars passing, I feel the vibrations in ground as they pass right by me, and if the car is old enough, I might even smell the gases expunged from the exhaust pipe. Somehow, all these sensory signals in all the modalities are integrated and I perceive a car passing as a coherent percept across all modalities. How the brain fuses the information from the different senses is one of the core questions of our perception and can in fact be formulated as two separate problems. The first is the question of how the information is interpreted to have one and the same causal origin i.e., how come I perceive it as one car passing instead of two or more cars, all individually generating one of the unimodal sensory signals? Second, how is this information integrated, i.e., having accepted that the visual input, sound, and vibrations all came from the same car in the example above, how are the signals from the different sensory modalities integrated in the brain? The latter has for decades been in the spotlight of multisensory perceptual research, sparked by findings dating back to the 1980s when Barry Stein and Alex Meredith discovered multisensory neurons in the superior colliculus in cats that responded to both visual and auditory stimuli (Meredith & Stein, 1986). Interestingly, the responses to multisensory stimuli were integrated in a superadditive manner, where the response to both visual and auditory stimuli (presented spatially congruent and within a limited temporal window) were larger than the responses to each stimulus presented alone. This superadditive integration became the hallmark mechanism of multisensory integration through which the brain amplifies biologically important stimuli. Since their discovery, other multisensory neuronal populations that integrate visual, tactile and proprioceptive signals have been discovered in both humans and non-human primates (Avillac et al., 2007; M. S. Graziano et al., 1997; M. S. Graziano & Gross, 1993; Michael S. A. Graziano et al., 2000; Rizzolatti et al., 1981). However, focusing purely on the integration of sensory information, without addressing which stimuli are integrated and the criteria for the integration misses out on the vital process of deciding to

which degree to integrate the stimuli or not, since all stimuli are clearly not integrated. In the example with the cars above, if I would see a car pass right by me while hearing a faint engine sound in the distance, it would not make sense to integrate these signals, since they most likely have two sources of origin, and luckily this does not happen (although the introduction of near silent electrical cars has fooled me once or twice). This indicates that prior to integrating multimodal stimuli, the brain decides which stimuli to integrate, which has been empirically observed and reported in multisensory experiments previously (referred to as the 'multisensory binding' or 'multisensory assignment' problem), but until recently was not formalized in the multisensory models. To this end, a computational theoretical framework based on probabilistic models of multisensory perception has been developed (Körding et al., 2007). Probabilistic models of multisensory perception are not new in the sense that similar ideas were first proposed by Hermann Von Helmholtz in the 19th century, where he in his "Handbuch der physiologischen Optik" (Treatise on Physiological Optics) (1856-67) proposed a probabilistic model of visual perception based on an integration of both prior beliefs and the actual sensory stimuli which he called "unbewusster schluss" (unconscious inference) (Helmholtz, 1867). The modern-day Bayesian causal inference model has striking similarities to this early framework, although it has been formalized in detail. In this causal inference framework, the brain solves the problem of multisensory binding by a process of causal inference, where the brain infers a common cause of stimuli based on spatial proximity, simultaneity, temporal correlation, and prior perceptual experiences, and, in turn, this inferred causal structure determines to what extent the sensory signals should be integrated (Körding et al., 2007).

The Bayesian causal inference model was initially proposed for bimodal audio-visual stimuli where the empirical evidence has shown a high compliance with the model (Körding et al., 2007) and almost a decade later, an adapted version of the model was proposed for the sense of body ownership (Samad et al., 2015). The proposed model was applied to the rubber hand illusion, designed as an integration of visual, tactile and proprioceptive signals relaying spatial and temporal information underlying the inference of body ownership (Fig. 1). Simulations of the model indicated that the inference to a common cause of the seen and felt touches would be made if the hands were within 30 cm of each other (spatial rule), and if the delivered seen and felt touches are synchronous (temporal rule). Interestingly, the model also predicted that inference to a common cause could be made in the absence of visuo-tactile stimulation, which the authors reproduce in an empirical experiment, however, methodological differences and the fact that the authors compare the subjective illusion ratings to a null result rather than to a control condition might explain why similar results have not been observed in other studies (Guterstam et al., 2019). Furthermore, the neural mechanisms and correlates of such a Bayesian

causal inference model was recently examined in a study on both macaques and humans (Fang et al., 2019). In this study, the premotor cortex was identified as a brain region that implements a form of Bayesian causal inference to the multisensory binding problem of body ownership. Taken together, this model proposes that a process of inference to a common cause happens in the rubber hand illusion (i.e., interpreting the visual and tactile signals as originating from the same hand) leading to the fusion of the visual, tactile and proprioceptive signals, which further causes a change in perceived hand location. In **Study I**, we wanted to investigate the causal relationship between changes in hand localization and the sense of body ownership in the rubber hand illusion. In particular we wanted to examine whether the recalibration of hand position sense towards the rubber hand was a necessary condition for experiencing the rubber hand illusion or not, since as opposed to the causal inference model, some of the competing neurocognitive models were based on either this assumption or predicted that changing the correspondence between felt and viewed hand position would impact the illusory sense of ownership (Botvinick & Cohen, 1998; Tsakiris, 2010).

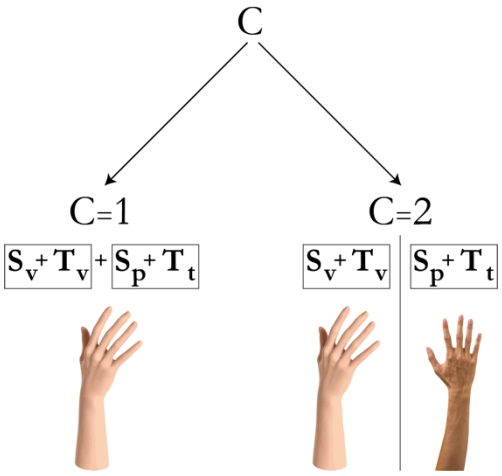


Figure 1. The causal inference model of body ownership proposed by Samad et al. (2015). Inference to a common cause (C=1) of the spatial and temporal visual signals from the rubber hand (S_v and T_v), spatial proprioceptive signals from the real hand (S_p) and temporal tactile signals from the real hand (T_t) leads to the sense of ownership of the rubber hand. The inference to separate causes (C=2) leads to the segregation of the signals arising from the rubber hand and the real hand, and no sense of ownership of the rubber hand ensues.

1.2.4 Neural correlates of body ownership

Lesion studies on patients with disturbances in the sense of body ownership have identified the frontal, parietal and temporal lobes (Feinberg et al., 2010; Vallar & Ronchi, 2009) as well as subcortical structures such as the basal ganglia (Halligan et al., 1993) and posterior insula (Baier & Karnath, 2008) to be involved the generation of a coherent bodily percept. However,

the neuroanatomical bases have only been outlined with a relatively low precision since the lesions usually span over several different functional brain regions and also involve subcortical structures, reducing the neuroanatomical specificity. Furthermore, inter-individual variations in the underlying anatomy as well as the shape and size of the lesion make group comparisons difficult. In light of this, recent studies on the neuroanatomical bases of the sense of body ownership have thus focused on electrophysiological studies in non-human primates as well as neuroimaging studies in humans aimed at identifying multisensory regions capable of performing the integration proposed to underlie the sense of body ownership.

Electrophysiological studies in non-human primates have identified neuronal populations in the frontal (M. S. Graziano et al., 1997; Rizzolatti et al., 1981) and parietal (Avillac et al., 2007; Michael S. A. Graziano et al., 2000) lobe that contain multisensory neuronal populations which integrate visual, tactile and proprioceptive signals. Furthermore, these neurons seem to have visual receptive fields (RF) that extend beyond the physical borders of the body to include the volume of space surrounding the body (M. S. Graziano, 1999), the so-called peri-personal space (Brozzoli et al., 2014). These RFs are anchored on the limbs, i.e., if the limb is moved, the RF of the specified neuron moves along with the limb and are unaffected by gaze direction (Fogassi et al., 1996; M. S. Graziano, 1999; M. S. A. Graziano & Gross, 1998). In macaques, these neurons have been identified in areas that are equivalent to the human premotor cortex, intraparietal sulcus (IPS) and posterior parietal cortices (PPC) as well as putamen (however, see (Culham & Valyear, 2006; Grefkes & Fink, 2005) for a cautionary reminder of such inter-species comparisons). Extending the work on non-human primates, neuroimaging studies on humans have identified brain regions that integrate body related visual-tactile-proprioceptive signals in fronto-parietal and cerebellar regions. The ventral premotor cortex (PMv), intraparietal sulcus (IPS) and supramarginal gyrus (SMG) as well as the cerebellum have been shown to display superadditive brain activity (measured as the BOLD signal, see methods) to bi-modal visual and tactile stimuli centered on the upper limb and furthermore that the same regions are responsive to stimuli presented in peri-personal space (Beauchamp et al., 2010; Gentile et al., 2011, 2013; Hadjikhani & Roland, 1998; Huang et al., 2012; Lloyd et al., 2003; Makin et al., 2007; Saito et al., 2003; Sereno & Huang, 2006). In a series of experiments, Brozzoli and colleagues showed that these areas displayed an adaptation to repeated visual stimuli close to the hand (Brozzoli et al., 2011), and furthermore that the activity in these areas is anchored on the hand, since the neural response shifted along with the hand when the hand's position was changed (Brozzoli et al., 2012). Such neuronal populations are the ideal candidates for the type of multisensory integration processes that have been proposed to underlie the sense of body ownership.

Consistent with these electrophysiological studies on non-human primates and neuroimaging studies on humans focusing on multisensory integration, fMRI experiments on human participants using bodily illusions as model systems for the sense of body ownership have identified the PMv, PPC, IPS and cerebellum to be involved in generating the sense of body ownership (H Henrik Ehrsson et al., 2004; Gentile et al., 2013; Grivaz et al., 2017; Guterstam et al., 2013; Limanowski & Blankenburg, 2016). These results have been reliably reproduced for individual limbs (H Henrik Ehrsson et al., 2004; Gentile et al., 2013), whole bodies (Gentile et al., 2015; Petkova et al., 2011) and new variations of the bodily illusions such as the invisible hand illusion (Guterstam et al., 2013). Apart from showing increased activity in those regions during the illusory experience of body ownership over a rubber hand or body, the activity in the PMv in particular has shown a correlation with behavioral outcome measures of the sense of body ownership (H Henrik Ehrsson et al., 2004; Gentile et al., 2013). Taken together, these results provide converging evidence that the sense of body ownership is reliant upon multisensory integration in brain regions housing neurons capable of such integration.

1.2.5 Disorders of body ownership

"She denied that the affected limbs were hers and said that 'yours' or another's were in bed with her. When she was shown that they were attached to her and that the arm in question merged with her shoulder and that it must be hers she said: 'But my eyes and my feelings don't agree, and I must believe my feelings. I know they look like mine, but I can feel they are not, and I can't believe my eyes" - C. W. Olsen, 1937, cited in Feinberg (2010)

Most healthy humans do not reflect over the existence of a sense ownership over their body and limbs, the feeling exists by default, and is only attended to once disturbances of it are evident. Such disturbances have been described in the neurological literature, where damage to frontal or parietal regions have been reported to lead to syndromes of asomatognosia or somatoparaphrenia (Critchley, 1953; Feinberg et al., 2010; Gerstmann, 1942; Vallar & Ronchi, 2009), where asomatognosia refers to the loss of ownership of a limb and somatoparaphrenia describes the loss of ownership of a limb combined with (often confabulatory) attribution of the limb to someone else (as captured in the quote above from Dr. Clarence W. Olsen at a meeting of the Los Angeles Neurological Society in 1937, cited in (Feinberg et al., 2010)). Apart from lesions in frontal and parietal regions, some lesion studies have also implicated the insula and basal ganglia (Baier & Karnath, 2008; Halligan et al., 1993) to be involved in the processes underlying the sense of body ownership. Worth noting is that these disturbances cannot be explained by impairments in unimodal vision or touch, since these patients can see their hand and sometimes also have intact tactile sensations from the hand. The correspondence

between these lesion studies and the neuroimaging studies combined with the fact that the displayed disability cannot be explained by unimodal impairments further strengthen the idea that the sense of body ownership is grounded in multisensory integration processes in these brain regions.

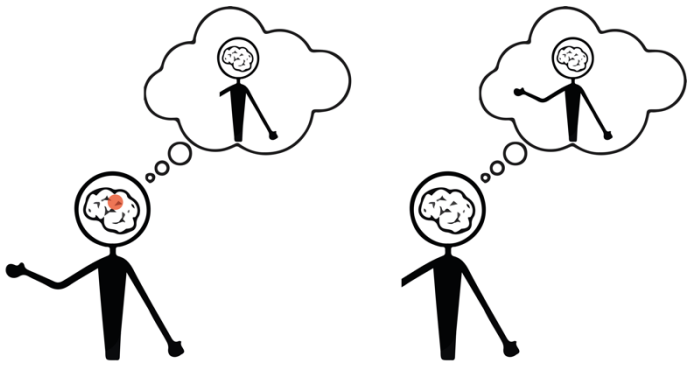


Figure 2. Illustration of two principally different disorders of body ownership. On the left, a patient with asomatognosia or somatoparaphrenia experiences no ownership of an existing physical limb, whereas on the right, an amputee experiences ownership of a physically non-existing limb.

While asomatognosia and somatoparaphrenia describes instances in which patients fail to attribute physical limbs to themselves, the opposite problem has been observed in amputees (Fig. 2). Following the amputation of a limb some patients report a vivid sensation of the limb still being attached to their body, and even more problematic, they can sometimes experience pain in this phantom limb (Ramachandran & Hirstein, 1998). Interestingly, after mapping out tactile stimuli on the stump, the rubber hand illusion can be induced in this patient population by brushing on the stump and corresponding places on the rubber hand, and the illusion is accompanied by neural activity in the same multisensory brain regions seen in healthy volunteers during the rubber hand illusion (H Henrik Ehrsson et al., 2008; Schmalzl et al., 2013). Furthermore, in some of these patients, inducing the rubber hand or virtual hand illusion can ameliorate the experience of and pain from the phantom limb (Chan et al., 2007; Ramachandran & Rogers-Ramachandran, 1996), highlighting some of the potential therapeutic applications of this research. Nevertheless, the precise relationship and perceptual and neural similarities between the illusory sense of ownership of the rubber hand and the experience of phantom limbs has yet to be investigated in detail.

1.3 THE SENSE OF AGENCY

1.3.1 What is the sense of agency?

In natural things, agent is often said of the principle of another's motion insofar as it is other. By motion, we mean here whatever passes from potency to act in a given matter.

- Ibn Sina (Avicenna), Kitāb al-Shifā (*Book of Healing*, *1027)*

Looking at our hands again, we might notice that aside from the feeling that the hands are ours (body ownership), when we move them, we also feel that we can control them, we get a sense that we are the agents performing the action. This sense of controlling one's actions and through them events in the outside world is the most commonly used definition of the sense of agency (Haggard, 2017; Haggard & Chambon, 2012). Although in our everyday lives and actions, this feeling is phenomenological thin, we become highly aware of it in situations of mismatch between what we intended to do and what actually happened. Historically, the sense of agency has been studied in paradigms aimed at elucidating the feeling of control of external events, namely the sensory feedback from button presses or manipulation of physical controllers, for example by having participants press a button and receive an auditory tone or visual flash feedback, or control a mouse or cursor on a screen (Fourneret & Jeannerod, 1998; Christopher D. Frith et al., 2000; Haggard et al., 2002; J. Moore & Haggard, 2008; Voss et al., 2010). The sense of agency is in these cases perturbed by manipulating the sensory feedback, for instance by excluding the tone feedback or introducing incongruencies in the movement of the cursor. Through these experiments, the sense of agency has been studied both behaviorally and neurally. Behaviorally, these experiments have elucidated some perceptual rules of the sense of agency, including the action rule (i), the temporal rule (ii) and the spatial rule (iii). The action rule (i) proposes that the sense of agency is reliant on active movement generation, without performing any movement, for instance in passive movements, the sense of agency is less likely to be present (Haggard & Chambon, 2012; Synofzik et al., 2008). The temporal rule (ii) states that the temporal relationship between action and sensory feedback needs to be consistent and without large delays, since both large delays (over 150 ms) and unpredictable delays have been shown to decrease the sense of agency (Daprati et al., 1997; Daprati & Sirigu, 2002). Finally, the spatial rule (ii) states that the action (or the expected outcome of the action) and the actual outcome need to be spatially congruent, for instance if the cursor on the screen moves to the left when the agent moved the mouse to the right, this would constitute a spatial incongruency that impairs the sense of agency. Such spatial incongruencies seem to be tolerated if they are kept below an orientation mis-match of 15 degrees (Farrer, Franck, Georgieff, et al., 2003; Farrer, Franck, Paillard, et al., 2003; Franck et al., 2001).

Similar to the sense of body ownership, the sense of agency also struggles with the same issues of how to be quantified. One way to quantify the sense of agency is to simply ask the participants or have them rate a set of statements regarding the experience of agency. However, such explicit judgements are subject to cognitive bias, task compliance and suggestibility, and in fact, studies have shown that participants are more prone to self-attribute actions if the outcome is positive (Bradley, 1978). Furthermore, explicit measures tend to reduce the sense of agency to a judgement of agency, a reduction that is not uncomplicated and has led some authors to propose a distinction between a pre-reflective low-level form av agency and a reflective (explicit) form of agency (Synofzik et al., 2008). In this thesis, I will refrain from making such a distinction, since only explicit behavioral measures of agency were used in the included studies. However, to avoid the pitfalls associated with explicit agency judgements, a lot of the literature on the sense of agency have used implicit outcome measures of agency. One of the most widely used is the so-called intentional binding paradigm, in which the perceived time between an action and its sensory consequences is compressed in situations of a high sense of agency compared to control conditions (Haggard et al., 2002; J. W. Moore & Obhi, 2012). In essence, the intentional binding paradigm is based on the assumption that self-generated actions and outcomes will be causally associated, leading to the perception of the action happening later in time than in actually did, and perception that the outcome happened earlier in time than it did (Fig. 3) compared to actions that are not followed by any outcome and outcomes that are not preceded by any action. Furthermore, the perceived compression of time between action and outcome is smaller in passive movements, while involuntary movements have even been showed to expand the perceived time between action and outcome (Haggard & Clark, 2003). Intentional binding has shown a high correlation with the subjective judgement of agency and has been widely used as a proxy for the implicit sense of agency (Ebert & Wegner, 2010; Haggard, 2005, 2017; Haggard et al., 2002; Haggard & Chambon, 2012; J. W. Moore & Obhi, 2012; Tsakiris & Haggard, 2003; Wolpe et al., 2013) (but see (David et al., 2008; Obhi & Hall, 2011; Synofzik et al., 2008) for arguments against the use of intentional binding as a proxy for the sense of agency).

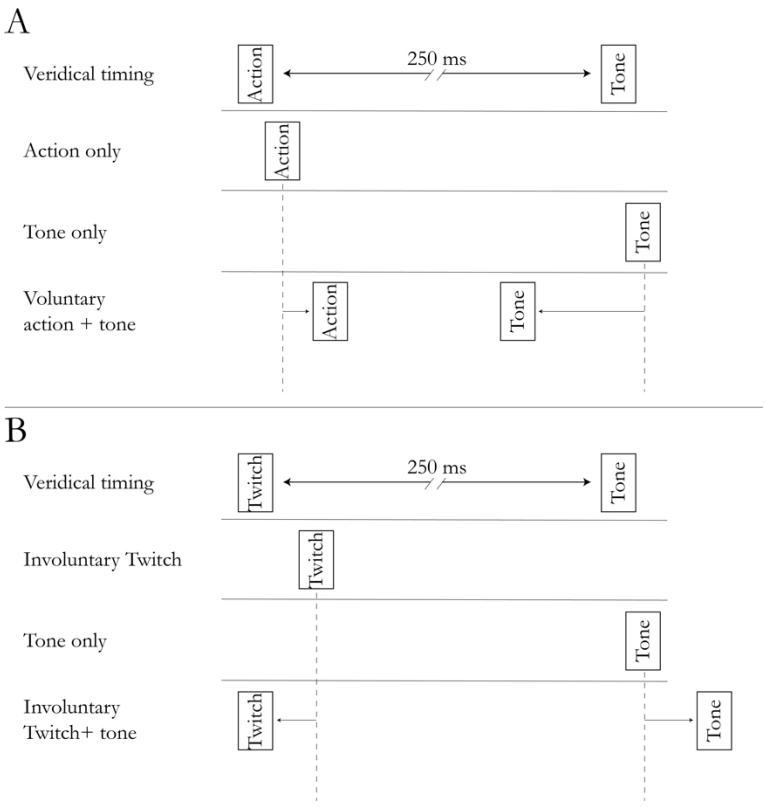


*Figure 3. Schematic illustration of the intentional binding paradigm. In **A** the participants press a button an receive a tone feedback. The perceived timing of the button press and tone will be closer to each other in trials when the button press produces a tone than in trials with either just a button press or just a tone. In **B,** the participants receive transcranial magnetic stimulation over the primary motor cortex, generating a twitch in their finger, which in turn produces a tone feedback. The perceived timing of the twitch and tone are farther from each other in trials with his involuntary twitch and tone than trials with just the twitch or just the tone. Illustration based on Haggard & Clark (2003).*

1.3.2 The comparator and beyond

"I trust that I now have made clear what the 'idea of a movement' is, which must precede it in order that it be voluntary. It is not the thought of the innervation which the movement requires. It is the anticipation of the movement's sensible effects, resident or remote, and sometime very remote indeed" – William James, Principles of psychology (1890)

The most popular model of the sense of agency draws inspiration from motor control theories, in particular the so-called comparator model, which was initially developed to describe how the brain monitors and correct goal directed action (Sarah-Jayne Blakemore et al., 2002; Christopher D. Frith et al., 2000; Wolpert & Kawato, 1998). The comparator model describes the sense of agency as arising following a comparison between the predicted and actual sensory feedback. This theory is grounded in the conception that somewhere between the decision to perform an action and generating the movement, a copy of the planned action is generated in

the brain. This so-called efference copy is used to compute a prediction of the sensory changes that would accompany the intended action, analogous to the "idea of a movement" proposed by William James in the quote above (James, 1890). This sensory prediction is then compared to the actual sensory feedback, and if the predicted and actual sensory feedback match, a sense of agency of the action is generated. This implies the sense of agency is a retrospective self-attribution of one's actions and is supported by the fact that perturbing the sensory feedback decreases the sense of agency while priming the participants with the outcome increases the sense of agency (Aarts et al., 2005; S. -J Blakemore et al., 2003; Sarah-Jayne Blakemore et al., 2002; Farrer, Franck, Georgieff, et al., 2003). However, some experiments have suggested that the sense of agency is also computed partly by a prospective component, where implicit measures of agency indicate that some form of agency is independent of the actual sensory feedback. In one experiment, participants performed an action and received a tone feedback in only some of the trials. The intentional binding showed that participants experienced the time at which an action occurred to be later in blocks which had a high probability of a tone following an action (75%) compared to blocks with a low probability of a tone following the action (50%), even in trials where no tone was presented (Fig. 4), indicating the presence of a prospective component of agency that operates in the absence of reafferent sensory information and is modulated by the predictability of the outcome (Voss et al., 2010).

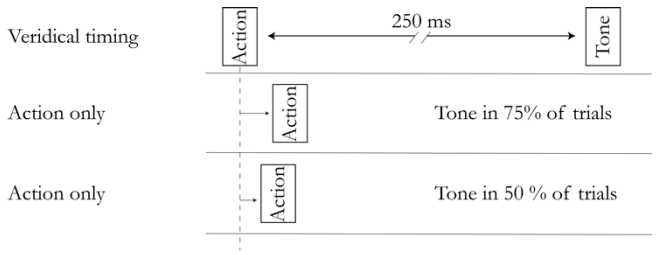


Figure 4. The prospective component of agency. The figure schematically illustrates the results from (Voss, 2010), wherein participants had two conditions of stimuli, one in which there was a high probability of a tone following an action (75%) and one in which there was a low probability of a tone following an action (50%). The binding of the perceived timing of the action closer to the tone happened even in trials with no tone, which is shown in the figure. Interestingly, the binding was significantly larger in the condition with the high predictability of tone feedback compared to the condition with low predictability.

Furthermore, the comparator model fails to encompass instances in which agentive experiences arise without the generation of any motor commands. For instance, it has been shown that participants in a pantomime task, where the participants see the hands of another person performing actions can experience agency over the viewed actions, as long as a predictive

account of the movements can be made, for instance by giving the participant verbal instructions for impending actions (Wegner et al., 2004). The sense of agency experienced in this situation cannot be accounted for by the comparator model since no movements are being made by the participants. One might argue that by viewing another person's hands in the anatomical positions of one's own hand performing an action while hearing predictions of the actions might entail motor imagery or other anticipatory processes, which might produce the sensory predictions necessary for the comparator model. However, this would indicate that either the efference copy is not as precise as previously thought (i.e., it is not a precise representation of the motor commands), or there are other processes independent of efference copies that can account for such predictions of sensory feedback, at the expense of losing the very characteristic of the comparator model, namely the comparison between efference copy-based predictions and the actual sensory feedback (Fig. 5). Intriguingly enough, a recent study on sensory attenuation, whose model to a large extent is based on the same efference copy-based predictions of sensory feedback as the comparator model, has shown that attenuation effects are seen with motor imagery devoid of any actual motor output (Kilteni et al., 2018). These results indicate that motor imagery can produce detailed and precisely timed information used to calculate the sensory predictions. However, whether these results translate to the sense of agency remains to be investigated.

In general, what was lacking in the literature was a coherent model of the sense of agency that takes into account prior knowledge and predictions as well as reafferent sensory signals and integrates and weighs this information in the process of generating agentive experiences. In a recent paper, Legaspi and colleagues, use the intentional binding paradigm as a model system for the sense of agency to propose a causal inference model of agency (Legaspi & Toyoizumi, 2019). The proposed Bayesian causal inference model integrates the sensory predictions and reafferent sensory signals (and weighs them according to reliability) which in turn infers causality of the events or not. Their model could account for the intentional binding effects from both (Tsakiris & Haggard, 2003) who showed decreased intentional binding in non-voluntary movements, and (Wolpe et al., 2013) who showed that decreasing the reliability of the tone feedback decreased the shift in perceived action timing towards the tone. In essence, the proposed model suggests that given a strong prior and noisy sensory feedback would lead to the estimate of agency relying more on the prospective component (i.e., prior known causal relationships) whereas a weak prior and reliable sensory feedback would lead to the estimate of agency relying more on the retrospective component, a notion consistent with Bayesian probabilistic models (Chater et al., 2006; Körding & Wolpert, 2006). Interestingly the proposed model also suggests that if the sensory signals are reliable enough, a sense of agency can

emerge for unintended actions, which serves as an empirical prediction that can be tested to validate the model.

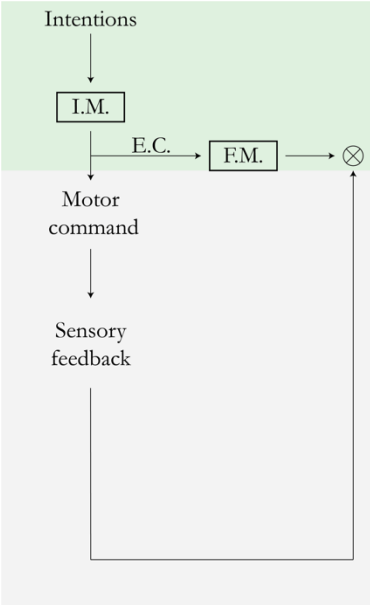


Figure 5. The comparator model of agency. Intentions are transformed to motor commands through a "inverse model" (I.M) which also generates an efference copy (E.C) used by the "forward model" (F.M) to create sensory predictions which are compared to the actual sensory feedback. The green field represents the processes that happen before the action, and thus represent the prospective component of agency, whereas the grey field indicate the processes after action execution, thus representing the retrospective component of agency. The "priors" in the causal inference model of agency is thus contained within the green field, since they represent the predictive components of agency.

1.3.3 Action awareness, intentions and causality

Wittgenstein famously asked, "What is left if I subtract the fact that my hand goes up from the fact that I raised my hand?" (Wittgenstein, 1953). One obvious answer to this is intention. When comparing voluntary and involuntary movements of our limbs, one thing that stands out is the presence or absence of the intention to move. Ranging back to the seminal study by Jonathan Libet and colleagues (Libet et al., 1983), neuroscientist and psychologist have tried to decipher the neural correlates of intention. Using a setup where participants are asked to perform an action, while watching a rotating clock hand, and retrospectively indicating the point at which they decided to move, have enabled researchers to identify the so-called readiness potential (RP) (Libet et al., 1983; Shibasaki & Hallett, 2006). Using electroencephalography (EEG) and electrocorticography (ECoG), researchers managed to identify an increase in neural activity some hundred milliseconds up to one second before the participants actually moved (Ikeda et al., 1992; Shibasaki & Hallett, 2006; Yamamoto et al., 2004). Interestingly, this RP is absent when patients with Gilles de la Tourette's syndrome

(commonly known as Tourette's syndrome) display uncontrollable motor and vocal tics but is present when the same patients are asked to voluntarily mimic their tics, linking the RP to the processes underlying intention (Karp et al., 1996; Obeso et al., 1981). Since the RP is intimately linked to intention which precedes the action itself as well as the sensory feedback, it serves as a potential substrate for the processes underlying the prospective sense of agency. The prospective component of agency can thus be conceptualized as arising following a comparison between the intentions and the predicted sensory feedback (Synofzik et al., 2008), prior to the comparison with the actual sensory feedback. Interestingly, such a comparison was actually proposed in the latest version of the comparator model (C. Frith, 2005; Christopher D. Frith et al., 2000) (although it was not proposed to be involved in the self-attributing process but rather in the updating of the inverse model). This has some interesting implications, because in order to have a forward model generating congruent predicted sensory feedback, there has to be some kind of established causality, i.e., the sensory feedback from the actions need to have an a priori established causal link to the actions. If the a priori causal link between action and outcome is weak, then the sense of agency of the action would be lower – imagine walking into a room and flicking the light switch, and instead of the light turning on, the Swedish national anthem starts playing. In this case, there is no temporal or spatial incongruency between action and outcome, but their causal contingencies based on prior experiences is low, which would likely impair the sense of agency, and many of us would probably assume the action and outcome to be unrelated and only coincided by accident. This hypothesis was tested by comparing the perceived sense of agency in trials with a high predictability of action outcomes compared to trials with low predictability of action outcomes. The perceived sense of agency was significantly higher in the high predictability group (A. Sato, 2009), consistent with similar effects observed for intentional binding (J. Moore & Haggard, 2008; Voss et al., 2010). Furthermore, Sato and colleagues show that priming participants with either congruent, incongruent or neutral primes in relation to the outcome of the action associated with a key press modulated the sense of agency more in the high predictability trials than in the low predictability trials, indicating that the prospective and retrospective components are integrated and weighted to produce a coherent sense of agency (A. Sato, 2009). These causality dependent predictions seem to be highly flexible, where causal contingencies has been shown to be updated on a trial to trial basis (J. Moore & Haggard, 2008).

As stated above, the Bayesian causal inference model of agency predicted that a sense of agency could arise for unintended actions, which begs the question of whether it is possible to have voluntary, but unintended actions? Previous studies have shown that it is possible to generate voluntary actions without the awareness of any active intentions to move the limb in

said matter, but rather the intention was aimed at some other task, which as a by-product generated a voluntary action leading to a movement of the limb (Newport & Gilpin, 2011; Stone et al., 2018). The interesting question remained of whether these actions without aware intentions would update the sensorimotor system in the same manner as aware actions, which has some implications for the explanatory models used to explain these sensorimotor recalibrations. In the prism adaptation literature, it has for long been known that active voluntary movements generate a larger, faster and more reliable visuo-proprioceptive recalibration compared to passive movements during the wearing of prism glasses that displace the visual field (Beckett, 1980; Fernández-Ruiz et al., 2004; Rossetti et al., 1998; Welch et al., 1979). This difference has been attributed to salient error signals which update the visuo-proprioceptive maps more during active than passive movements, grounded in a hypothesized distinction between intersensory and sensorimotor mismatch. (Chapman et al., 2010; Rossetti et al., 1998). In **Study III**, we wanted to investigate whether the same pattern of increased recalibration is seen in active conditions without any aware intentions nor any aware actions and compare this to passive conditions without any aware movements. This would indicate whether awareness of intention or movement is necessary for these recalibration mechanisms.

1.3.4 Disorders of agency

Most research on the sense of agency in clinical populations has been done on patients suffering from schizophrenia, where symptoms such as delusions of control and thought insertion have been attributed to disturbances in the neural mechanisms underlying the sense of agency (Daprati et al., 1997; Synofzik et al., 2010; Synofzik & Voss, 2010). In short, the theories postulate that schizophrenic patients fail to self-attribute thoughts, feelings and ideas and instead interpret them as originating from external agents. Rephrased within the comparator model framework, their ability to make adequate sensory predictions is impaired (Chris D Frith et al., 2000). Schizophrenic patients have been shown to be more prone to attribute viewed external actions to themselves than healthy controls, indicating an impairment in making self-other distinctions (Synofzik et al., 2010). Furthermore, these findings are supported by behavioral data using the intentional binding paradigm, where schizophrenic patients have been shown to have increased intentional binding compared to a control group, and that they do not display the same modulation by the probability of tone presentation as the healthy volunteers, but instead seem to rely more on retrospective components for agency judgements (Voss et al., 2010). The impairment in the ability to make adequate sensory predictions is corroborated by findings from the sensory attenuation literature, which is based on the notion that healthy individuals perceive the sensory effects of their own actions as weaker than externally produced

sensory effects. Schizophrenic individuals display a pattern of less attenuation to self-generated sensory signals (S. J. Blakemore et al., 2000; Shergill et al., 2005), indicating that schizophrenic patients have impairments in generating adequate sensory predictions of their actions, which is likely to mainly impair the prospective component of agency.

Other neuropsychological populations where disturbances in the sense of agency has been proposed to be central for the displayed disability is in patients suffering from the anarchic hand syndrome. The anarchic hand syndrome is usually associated with focal lesions in the frontal lobe, parietal lobe and corpus callosum as well as with neurodegenerative diseases such as corticobasal degeneration (Biran & Chatterjee, 2004; Doody & Jankovic, 1992; Fisher, 2000; Pacherie, 2007; Sala, 1998). The patients describe a loss of control over the actions of their hand and that it can perform actions without their intentions. Since these anarchic movements are perceived as involuntary, the sense of agency of them is diminished and patients sometimes even attribute the movements to an external agent, as captured in one of the earliest accounts of a patient with an anarchic hand syndrome, where a patient that had undergone a corpus callosotomy complained of repetitive unintentional grasping and attributed the movements to an external agent by stating that "there must be an evil spirit in the hand" ("Es muss wohl ein böser Geist in der Hand Sein") (Goldstein, 1908). Interestingly, neuroimaging studies have found the anarchic hand movements to be associated with isolated activity in the primary motor cortex (Assal et al., 2007; Schaefer et al., 2010), lacking activity in the frontal motor areas normally seen with voluntary action. Furthermore, transcranial magnetic stimulation over the motor cortex, generating a movement in the arm of healthy participants, is experienced as involuntary and participants report a lack of agency over said movement (Haggard & Clark, 2003; Tsakiris & Haggard, 2003). Conversely, electrical stimulation of the supplementary motor area (SMA) sometimes produced a feeling of an urge to move, without producing any movement (Fried et al., 1991), suggesting that intention and action planning in regions in the frontal lobe is part of the network that generates the predictions used for the processes underlying the sense of agency.

1.3.5 Neural correlates of agency

Given the proposed models for agency suggested above, the investigations of the neural correlates of the sense of agency have focused on identifying brain regions associated with intention and action planning as well as regions capable of performing the comparisons between predicted and actual sensory feedback. Areas involved in intention and action planning such as the supplementary motor complex (SMA and pre-SMA) and premotor cortices have been suggested to be involved in the prospective component of agency (Cavazzana et al., 2015; Haggard, 2017; J. W. Moore et al., 2010), whereas multisensory regions receiving both motor and sensory input such as the posterior parietal cortex as well as regions involved in coordination such as the cerebellum have been proposed to be involved in the retrospective component of the sense of agency (Chambon et al., 2013; David et al., 2008; Farrer, Franck, Georgieff, et al., 2003; Farrer & Frith, 2002; Kang et al., 2015; Schnell et al., 2007; Uhlmann et al., 2020; Yomogida et al., 2010).

Ever since the seminal studies on the neural substrates of the sense of agency by Farrer and colleagues (Farrer, Franck, Georgieff, et al., 2003; Farrer & Frith, 2002), there has been a tradition in the field of research on the sense of agency to make use of a paradigm with various degrees of temporal or spatial mismatch between action and outcome. The analyses have often focused on identifying the brain regions that display increased activity with increased mismatch, i.e., regions responsive to the loss of the sense of agency. These studies have identified the posterior parietal cortex, and in particular the right angular gyrus to be related to the loss of the sense of agency (David et al., 2008; Farrer, Franck, Georgieff, et al., 2003; Farrer & Frith, 2002; Yomogida et al., 2010). It is worth mentioning that these studies implemented some kind of temporal or spatial mismatch between action and sensory feedback in active movements, meaning that aside from a sensorimotor mismatch, there is also an inter-sensory mismatch, since they do not include passive control conditions. This has to be taken into account when interpreting these results since some studies have indicated that the angular gyrus is responsive to sudden changes in multimodal sensory signals (Downar et al., 2000), which could confound these findings. The few studies that have investigated the neural correlates of the positive experience of agency, i.e., regions that display increased activity in response to increased action-feedback congruency have identified the insula to be associated with the experience of agency (Farrer, Franck, Georgieff, et al., 2003; Farrer & Frith, 2002). Finally, a meta-analysis identified the angular gyrus to be associated with the loss of agency, while the

anterior insula and the left pre- and post-central gyrus were associated with the positive experience of agency (Sperduti et al., 2011).

However, what most of these studies lack is the investigation of agency over one's body, i.e., the sense of agency in the presence of body ownership and how this differs from agency of external objects and events. When we perform a voluntary action, it necessarily involves some kind of macroscopic movement of our bodies or limbs, which in turn will generate some kind of sensory feedback from the body (tactile, proprioceptive, visual) before the external effects of the action generates any sensory feedback. Until the discovery of the moving rubber hand illusion, separating the two was difficult. To examine this, we conducted **Study IV**, a behavioral and neuroimaging study to investigate the sense of agency in a bodily context.

1.4 THE SENSE OF BODY OWNERSHIP AND THE SENSE AGENCY – ADDITIVE OR INDEPENDENT?

In our everyday lives we usually experience our bodies to encompass both the sense of body ownership and a sense of agency. We feel that our body belongs to us, and that we can control it. This experience does not need to be particularly salient or even conscious throughout the day, but rather just exist as a background common state. However, there is a clear dissociation between the feeling of ownership and the sense of agency when our body parts are passively moved. In that situation, we do not enjoy a sense of agency (since we did not perform or intend to perform a movement) but the sense of ownership does still remain anchored to the body part. The whole line of studies on intentional binding and the sense of agency indicate that the sense of agency is closely linked to efference copy-based predictions, whereas the feeling ownership can be induced using purely afferent signals (e.g., the rubber hand illusion). So, the question is, how do these two phenomena, the feeling of ownership and the sense of agency relate to one another? One view is that they are additive, i.e., that agency entails ownership (Tsakiris et al., 2007). Since the sense of agency has been thought to require voluntary action, which can only be applied to the own body, this would include strong efferent and afferent cues, which would induce a feeling of ownership. This view then proposes that the sense of agency includes the feeling of ownership, plus some additional feeling of voluntary control. This has some interesting predictions regarding the neural correlates of agency and ownership, it predicts that agency and ownership have overlapping neural activations and further that the neural correlates of ownership are a subset of those of agency. The competing proposal on the relationship between the sense of body ownership and agency hold that they are two independent processes that rely on qualitatively distinct neural mechanisms. This model draws support from the

observation that paralyzed patients do not commonly report disturbances in the sense of body ownership as well as from recent behavioral experiments on the moving rubber hand illusion that have shown a behavioral dissociation of the two phenomena (Kalckert & Ehrsson, 2012, 2014a). These findings support predictions about the neural correlates of ownership and agency that are separate (although some possible overlap cannot be completely ruled out). Comparing these two different models, one interesting question is whether agency of the own body obeys the same rules and is based on the same mechanisms as agency of external objects. If the sense of agency always entails ownership, then agency of the own body would not differ in terms of perceptual and neural mechanisms from agency of external objects, whereas if the sense of body ownership and agency are independent and interact in the case of agency over the body, the perceptual and neural mechanisms of agency over the body or external objects would differ. In **Study IV**, we devised a setup in which we can create a double dissociation between ownership and agency using the moving rubber hand illusion, and thus directly compare the neural correlates of the sense of agency of the body and the sense of agency of external objects.

2 AIMS

2.1 STUDY I

Study I investigated the causal relationship between changes in hand position sense (i.e., the proprioceptive drift) and the subjective sense of body ownership in the rubber hand illusion.

2.2 STUDY II

The aim of study II was to investigate the permanence and decay of the proprioceptive drift and the subjective sense of body ownership after the end of the visuo-tactile stimulation in the rubber hand illusion.

2.3 STUDY III

Study III aimed at elucidating if the visuo-proprioceptive recalibration of hand position sense differs between unconscious active and passive movements.

2.4 STUDY IV

Study IV aimed at investigating the neural correlates of the sense of body ownership and the sense of agency as well as their interaction.

3 METHODS

3.1 PARTICIPANTS

A total of 118 healthy participants were included in **Study I-IV**. All participants were naïve to the specific purposes of the experiment they participated in. Prior to participating, informed consent was obtained from all participants. The experiments were conducted in accordance with the declaration of Helsinki and approved by the Swedish Ethical Review Authority.

3.2 QUESTIONNAIRES

Throughout **Study I-IV**, questionnaires have been used to various extents to quantify the subjective experiences. Questionnaires aimed at quantifying the subjective experience of body ownership were presented after each experimental condition, whereas questionnaires aimed at probing the level of conscious perception of movements (**Study I & III**) were presented at the very end of the experiment. In some cases, where the experimental paradigm did not allow enough time to rate several statements, a shorter version or a single representative question aimed at probing one aspect of the illusory experience (**Study II & III**) was presented. The questionnaires aimed at evaluating the sense of body ownership were designed based on the original rubber hand illusion study (Botvinick & Cohen, 1998), which has since been used and replicated in multiple studies on body ownership (Abdulkarim & Ehrsson, 2016; Kalckert & Ehrsson, 2012), whereas the questionnaire evaluating the sense of agency (**Study IV**) was based on the moving rubber hand illusion study (Kalckert & Ehrsson, 2012). In general participants were asked to affirm or deny a set of statements probing various aspects of the illusory experience on a 7-point Likert scale ranging from (-3) corresponding to "completely disagree" to (+3) corresponding to "completely agree", where (0) corresponds to "neither agree nor disagree".

Probing subjective experiences with questionnaires like this is not uncomplicated. Task compliance, suggestibility and cognitive biases are all potential confounders of the results, and to this end the questionnaire needs to be carefully designed to include efficient control statements, which were designed to be as similar as illusion statements as possible, but instead probing perceptual effects that we hypothesized would not be present. Furthermore, the comparisons of the questionnaire results were always done between conditions. In this way control conditions that were manipulated by one key factor (for instance visuo-tactile synchrony) that abolished the illusion, while keeping all other factors constant could be used to control for the potential confounders. Finally, the questionnaires were always used in

conjunction with or by comparison to implicit measures of body ownership such as the proprioceptive drift.

3.3 PROPRIOCEPTIVE DRIFT

The proprioceptive drift has been one of the most widely used implicit measures of the rubber hand illusion and has been shown to correlate with the illusory experience (Botvinick & Cohen, 1998; Costantini & Haggard, 2007; H. Henrik Ehrsson et al., 2005; Guterstam et al., 2013; Kalckert & Ehrsson, 2014b; Longo et al., 2008; Samad et al., 2015; Tsakiris & Haggard, 2005). The proprioceptive drift describes the change in hand localization that becomes apparent when comparing perceived hand localization prior to and after the induction of the rubber hand illusion (Botvinick & Cohen, 1998). There are different ways to measure hand localization by indicating the perceived position of one's hand, including verbal reports, pointing using a digital aid and an inter-manual pointing task. Differences in perceived limb location have been observed depending on which type of method was used (Kammers et al., 2006), which is why in **Study I-III**, we use the same inter-manual pointing task in which participants are asked to close their eyes and then use their contralateral hand to point to the location in which they perceive their hand to be located. Specifically, the participants were asked to close their eyes and slide their left index finger along a metal ruler extending over both the participants hand and the viewed hand until they felt they were immediately above their right index finger. The metal ruler had distance markings only visible to the experimenter, and the ruler was uniform in size and shape without any identifiable cues to where on the ruler the participants left index finger was. The statistical analyses were made by subtracting the perceived hand location prior to the trial from the perceived hand location immediately after the end of the trial. The resulting difference was entered into a t-test, ANOVA or Wilcoxon Signed Ranks test depending on the experimental design and distribution of the data, and further compared between conditions. We opted for this inter-manual pointing task for several reasons, amongst others, we believe that the inter-manual pointing task to be an implicit outcome measure and less subjected to cognitive bias than verbal reports. Furthermore, we reason that locating the limb in space with the contralateral hand is important for inter-manual coordination and hence more ecologically valid than verbally reporting perceived limb location.

3.4 HAND DISPLACEMENT APPARATUS

In **Study I & III**, we implemented the use of a new mechanical apparatus which allowed us to displace the participants hand passively without them noticing. The apparatus consisted of a platform on which the participants rested their hand which was composed of two sheets of Plexiglas resting on plastic tubes which in turn rested on a rubber mouse pad. The platform was connected with a rack bar to a cog wheel which in turn was connected to a brushless electrical engine (Micro Motors E192.24.625, Verderio Inferiore, Italy). The apparatus could displace the participants hand either medially or laterally with a speed of 0.9 mm/s. The displacement was done slow enough and without any noticeable vibration for the displacement to pass by unnoticed by the participants. A questionnaire regarding the awareness of any displacement was filled out by the participants after the experiment. None of the participants could report any sensations of displacement and anecdotally, most participants would express surprise once learning that their hand had been displaced several centimeters repeatedly during the experiment.

3.5 HAND ILLUSION BOX

In order to study the visuo-proprioceptive recalibration in **Study III**, we had to design an experimental setup which allowed us to induce a sensorimotor illusion that included unconscious active movements made by the participants. To this end, we developed the Hand Illusion Box (HI-box). Using a set of mirrors, cameras, a high refresh rate 3D-display and 3D-goggles. We were able to create a sensorimotor illusion similar to the one described in the disappearing limb tricks (Newport & Gilpin, 2011; Stone et al., 2018). Seated in front of the hand illusion box and placing their hand inside the box, the participants would see their hand in 3D from a first-person perspective and with minimal delay (43 ms). The sensorimotor illusion was brought about by having the participants view their hand form the first-person perspective while asking them to hold their hand up in mid-air and keep it in the center of the screen. In the passive conditions, the participants were instructed to place their hand on the table, which consisted of the movable platform in the hand displacement apparatus from **Study I**, and simply relax while focusing on their hand. While holding their hand up in mid-air or resting it on the platform of the hand displacement apparatus in the active and passive conditions respectively, the viewed hand on the screen would start to shift medially. The shift was done so slowly that the participants did not notice it, and furthermore, in order to keep their hand in the middle of the screen in the active conditions, the participants would have to perform corrective movements laterally. In the passive conditions, the corrective movements were made by having the hand displacement apparatus displace the participants hand laterally without the

participants having to perform any movements. To obscure the shift, two blue fields were superimposed on the screen, slowly creeping inwards from the sides of the viewed hand until the field of view on the screen had shrunk to only include the hand. At this point, the participant's hand had been displaced 8 cm laterally, either actively or passively, and the participants were unaware of the displacement.

In **Study III**, we compared the change in the perceived hand localization between the active and passive conditions. The participants indicated the perceived hand localization as described in the proprioceptive drift measure above before and after their hand had been actively or passively displaced without their awareness of the displacement.

3.6 MOVING RUBBER HAND ILLUSION SETUP

In **Study IV**, we adopted the moving rubber hand illusion setup for the fMRI environment. In particular, the vertical setup of the illusion used in previous studies had to be abandoned for a horizontal setup in order to fit inside the scanned bore (Fig. 6, Panel E). Furthermore, the setup had to be completely non-ferromagnetic, which called for a replacement of all the metallic components in the flexible joints of the hand. To link the movements of the index finger of the rubber hand and the index finger of the participant in the horizontal setup, a new mechanical linkage using a series of levers and rods was designed (Fig. 6, Panel A). This setup allowed us to manipulate the synchrony, movement type (active or passive) and anatomical congruency of the rubber hand. By extracting the pin connecting the levers together (Fig. 6, Panel C-D) the movements of the rubber hand could be decoupled by from the movements of the participants hand (asynchronous condition). The movement type was manipulated by having participants move their fingers actively, or have the experimenter move their finger by pressing the rod connected to their finger up (Fig. 6, Panel B). The anatomical congruency of the rubber hand was manipulated by rotating the rubber hand 180 degrees.

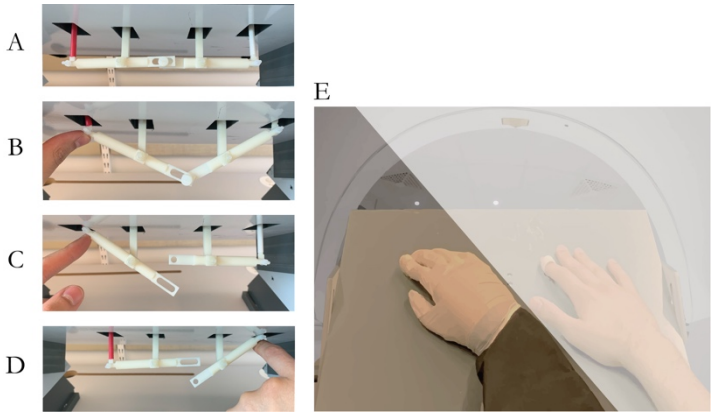


*Figure 6. Panel **A-D** illustrates the levers of the moving rubber hand illusion setup under the table that moved the index finger of the participant and the rubber hand. In **A**, the levers are in a relaxed position with the index finger of the rubber hand and the participant's hand resting on the table. In **B**, both the participants index finger and the index finger of the rubber hand is lifted off the table. The two levers are connected to each other through a pin. In this configuration the participants could lift their index finger, which would simultaneously lift the index finger of the rubber hand (active synchronous conditions), or the experimenter could push the index finger of the participant up by pressing on the rod underneath the participants index finger (as seen in the image; passive synchronous condition). In **C & D**, the two fingers have been decoupled by removing the pin holding the two levers together. In this configuration, the index finger of the rubber hand and the participants hand could be moved independently (active and passive asynchronous conditions). **E**. Depicts a montage of what the participants would see laying inside the MR-scanner. The white semi-opaque field illustrates the dark cloth used to cover the participant's real right hand from sight. The participant's hand and the rubber hand are seen resting on the small table. The index finger of the rubber hand as well as the participant's hand is placed inside a white plastic ring, which is connected to the two most lateral vertical rods seen in panel A-D.*

3.7 FUNCTIONAL MAGNETIC RESONANCE IMAGING

3.7.1 General

Functional magnetic resonance imaging (fMRI) is a non-invasive neuroimaging method which has gained increased popularity since its discovery in 1990 (Ogawa et al., 1990) and can be used to test specific neuroanatomical hypotheses in controlled experiments on healthy human volunteers. In contrast to anatomical MRI scans, the principle of fMRI rests on the so-called neurovascular reflex originally proposed by Charles Roy and Charles Sherrington who discovered that regional changes in blood flow to the brain could be observed in response to brain activity (Roy & Sherrington, 1890). In essence, the reflex is based on the notion that as neuronal populations in a brain region become activated, their metabolic demand increases. This leads to a higher extraction of oxygen from the blood and approximately 0.5 seconds after the increase in neuronal activity, the concentration of oxygenated hemoglobin decreases. The local decrease in oxygen in turn triggers a vascular reflex leading to dilation of local arterioles, which some 4-6s afterwards leads to an over-compensatory increase in the regional blood flow.

These changes in the regional blood flow is called the hemodynamic response function (HRF), which although it cannot be measured directly, does have measurable proxies in the form of different magnetic properties of oxygenated and deoxygenated hemoglobin. These magnetic differences can be measured inside the strong magnetic field of the MR-scanner by measuring the response to a radio frequency pulse transmitted into the heterogenic magnetic field. The resulting signal is called the Blood Oxygenation Level Dependent (BOLD) signal and allows the researchers to obtain a snapshot image of the blood flow in a section of the brain. Repeating the same procedure over multiple sections throughout the brain generates a three-dimensional volume of the whole brain with measured BOLD signals in three-dimensional pixels, so-called voxels. Modern MR-scanners can sample one volume of the whole brain every couple of seconds, and by continuously sampling whole brain volumes, the change in the BOLD signal of brain regions can be analyzed over time, albeit with a temporal resolution of a couple of seconds. The BOLD signal, although being an indirect measure of the regional blood flow which in turn is an indirect measure of neuronal activity, has been shown to be a reliable measure of brain activity which correlates with changes in the cerebral blood flow and blood volume (Goense et al., 2012) as well as with the local field potential (Logothetis et al., 2001).

3.7.2 Limitations

fMRI has provided cognitive neuroscientist, neuropsychiatrists and psychologists with a powerful tool to investigate neural activity related to cognitive tasks and pathology. However, there are some drawbacks with the method that warrants caution and careful planning of experiments. First of all, the temporal resolution in fMRI is relatively low compared to other neurophysiological measures (for instance EEG or ECoG) and the activity in the brain is sampled every couple of seconds, meaning that the experimental conditions need to be long enough to be able register the change in BOLD signal and be spaced with sufficient time between each condition to avoid carry-over effects. In **Study IV** we therefore used a blocked design, where each condition is repeated within a block for tens of seconds and followed by a break before the next condition. Blocked designs have been shown to increase the statistical power of the fMRI data analysis (Friston et al., 1999), while facilitating the design and analysis. Moreover, the data collection in fMRI requires the participants to be completely still, since the volumes of the brain containing the voxels of brain activity assumes that the voxels are static and that the same volume of brain tissue is sampled at every timepoint. To ensure that the participants did not move during the experiment, the participants were instructed to not move their head during the experiment and we also made sure that the participant's head was fixed inside the head coil of the MR-scanner by placing padding and foam pads around the

participant's head inside the head coil. Apart from these practical efforts to reduce head motion during the experiment, the software used to analyze the fMRI data (Statistical Parametric Modelling 12, SPM12, Wellcome Trust Center for Neuroimaging, University College London, UK) has an algorithm that corrects for motion during the preprocessing steps of the data analysis. The algorithm exports the realignment parameters which allowed us to inspect the head motion for every participant and in every run. We could not identify any head motion that was larger than the size of one voxel (2 mm) in our fMRI protocol in **Study IV**, and thus we did not exclude any volumes from the analysis.

Despite the clear advantages of the blocked fMRI design in regard to our experimental setup, there are some potential caveats. Since the experimental conditions are designed as blocks of repeated stimuli, the condition regressors entered into the analysis do not take into account variances in number or frequency of stimuli between conditions. Hence, the number and frequency of stimuli need to be carefully controlled across conditions to avoid that the results are confounded by such differences. In **Study IV**, participants made self-paced tapping movements with their right index finger; in order to control for the number and frequency of taps, participants were instructed to be consistent with the frequency of taps and were also trained with a metronome (1Hz) prior to starting the data collection. Moreover, we made use of an optical sensor placed under the index finger of the participant that could register whenever the participants lifted their finger off the table, and thus we could get a measure of the number and frequency of taps. We show that there are no significant differences in neither the number or the frequency of taps across conditions, and therefore feel comfortable that the results obtained are not driven by differences in the number of stimuli between conditions (Fig. 7).

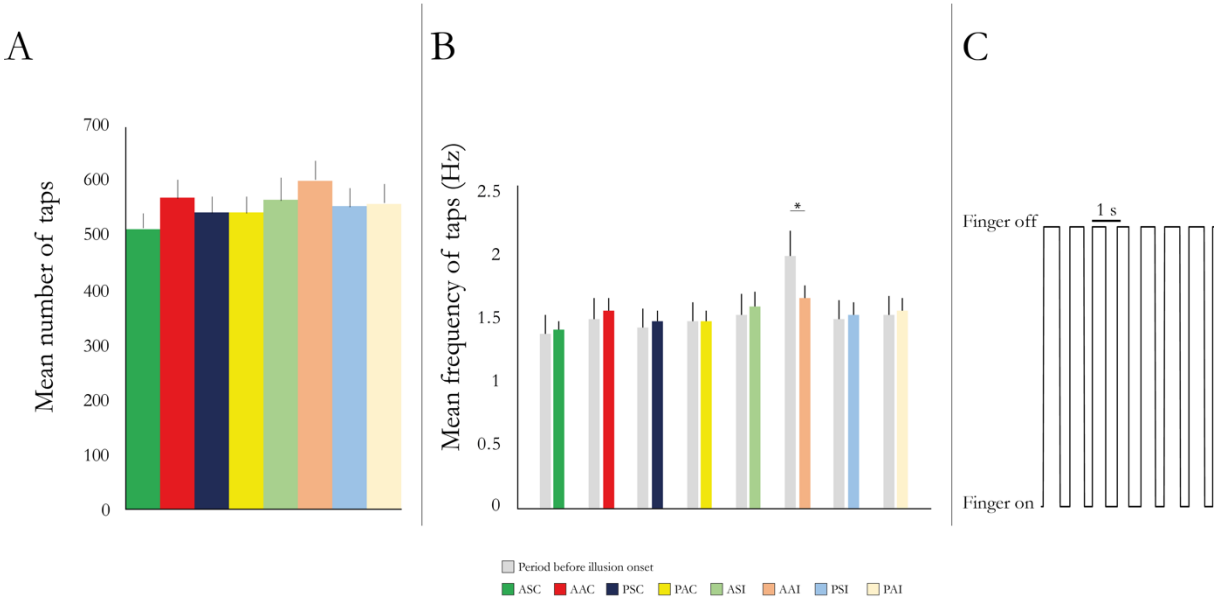


*Figure 7. To control for the number and frequency of taps across conditions we used an optical sensor to register the finger movements of the participants. **A** Shows the average number of taps during the entire experiments for each condition. In **B**, we show the frequency of taps split up by condition and time before illusion onset. In **C**, the individual taps from one participant (no 17) is shown, with the data from the optical sensor indicating when the participant's finger is lifted off the table ('Finger off') and when it is placed on the table ('Finger on').*

In **Study IV**, we employed a within-subjects 2x2x2 factorial design. We defined the factors synchrony (synchronous or asynchronous), movement type (active or passive) and anatomical congruency (congruent or incongruent) generating eight unique conditions. The benefit of this factorial design is that we can define specific contrasts as interactions between the factors with precise and efficient control conditions. The benefits of having proper control conditions by opting for this type of factorial design has to be weighed against the cost of having eight unique conditions, which includes prolonged scan time and increased complexity in the comprehension of the results. In the end, we opted to run the experiment using the 2x2x2 design, due to the fact that we were interested in the three-way interaction between synchrony, movement type and anatomical congruency, and we reasoned we had a robust plan for the analysis a priori.

3.7.3 Preprocessing

Prior to the statistical analysis, the fMRI data from all participants were subject to standard preprocessing steps. In **Study IV**, the participants lay inside the MR-scanner with their head tilted, therefore, the collected images had to be manually rotated back to a standard position. Following this, the standard preprocessing steps including motion correction, slice timing

correction, co-registration, re-slicing, normalization and smoothing was carried out on all functional images. The functional images were normalized to a standard Montreal Neurological Institute (MNI) brain, which allowed us to compare results between participants as well as compare our results with the previous literature using the same standardized MNI space. The images were resliced to a resolution of 2x2x2 mm and the smoothing was done using a 6 mm FWHM Gaussian kernel.

3.7.4 Univariate analyses

In the first-level analysis in **Study IV**, we defined regressors for each condition individually for every participant and run. The periods before illusion onset (using individually obtained time-to-illusion measurements) were modeled as regressors of no interest. Each experimental condition was modeled with a boxcar function and convolved with the hemodynamic response function in SPM12. Linear contrasts were defined at the individual level and then exported to the second-level random effects analysis.

3.7.5 The problem of multiple comparisons in fMRI

Statistical analysis of fMRI poses a challenge due to the large amount of data collected. Each participant can generate up to millions of data points which are entered into the statistical analysis, which makes inferences hard, and increases the risk of false positive results. Due to this, several different approaches to increase the statistical power while minimizing the risk of type 1 errors have been developed. In **Study IV**, we used a combination of two approaches. First, we looked for activity on the whole brain level, correcting for multiple comparisons using the more lenient so-called false discovery rate (FDR). Furthermore, based on the previous literature, we had anatomical hypotheses regarding certain brain regions, but due to differences in the experimental setup between our current study and the literature, we also conducted a pilot study with similar experimental manipulations as in **Study IV** and extracted the precise coordinates for the activation peaks within those brain regions. We then conducted analyses where we corrected for multiple comparisons using the more conservative family-wise error correction, (FWE) within a defined volume of space centered on those activation peaks. Some activations, that did not survive the whole-brain FDR correction, nor had any corresponding anatomical hypotheses that would warrant small volume FWE correction, we report for descriptive purposes only, and always indicate that they did not reach statistical significance after correction for multiple comparisons.

4 MAIN RESULTS AND CONCLUSIONS

In this section, I will briefly summarize the main results and conclusions from each study. For detailed results and an extended discussion, I refer the reader to the manuscripts attached at the end of this thesis.

4.1 STUDY I

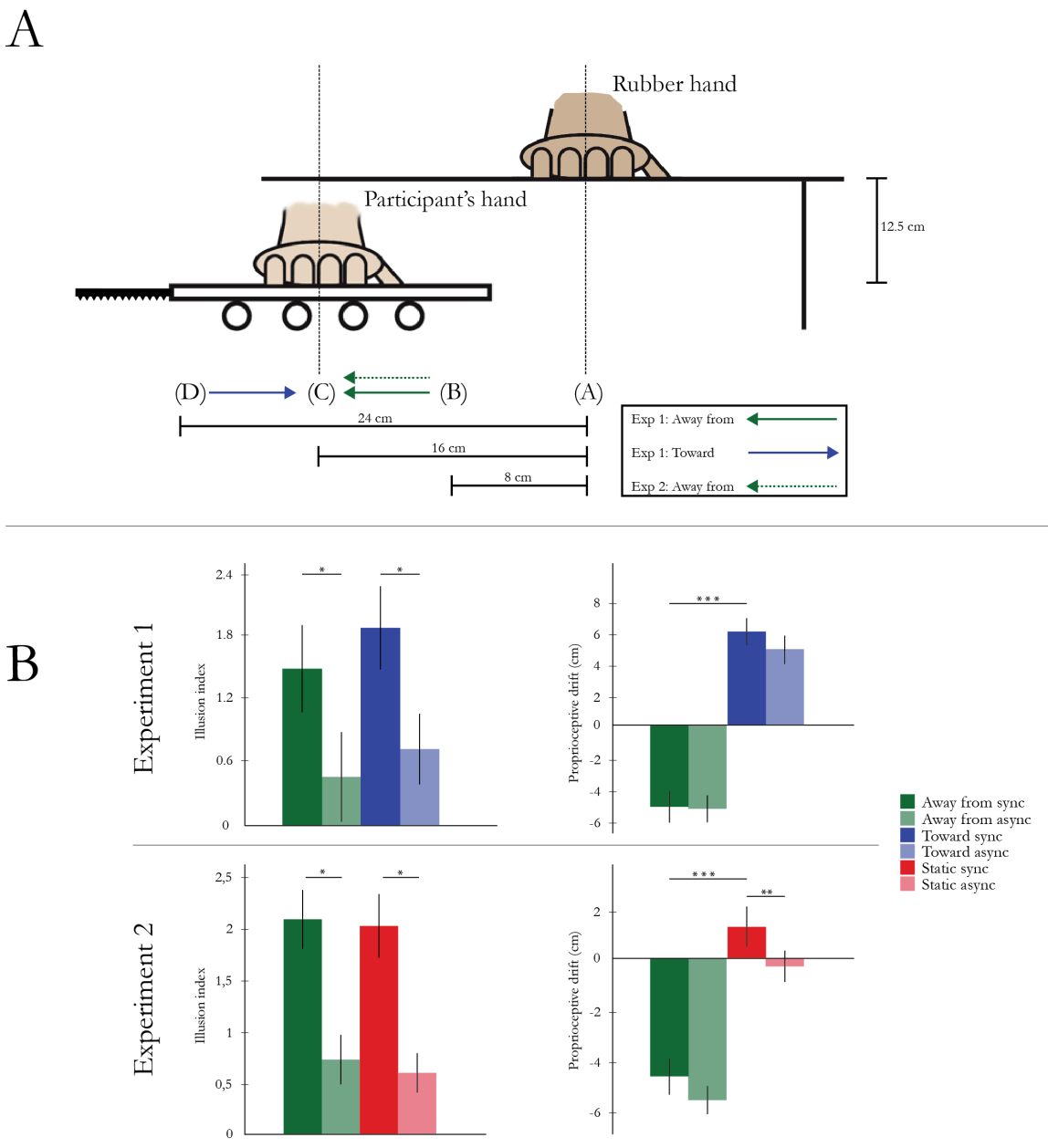


*Figure 8. The main methods and findings from Study I. **A** depicts the experimental setup. The rubber hand was placed on top of a small table under which the participants hand rested on the hand displacement apparatus. **B** In experiment 1 we showed that the sense of body ownership expressed as the illusion index (ownership ratings minus ownership control ratings) did not differ regardless of whether the spatial discrepancy between the participants real hand and the rubber hand had increased or decreased. In experiment 2, we replicate the findings for the condition in which the discrepancy increases and show that there is no difference between this and a static condition in which the participants hand was not moved at all. Note that the displacement of the participants hand was done without them noticing the displacement, but the change in location of their displaced hand is apparent in the hand localization task used to calculate the proprioceptive drift. Drifts >0 indicate a change in hand localization toward the rubber hand, whereas drifts <0 indicate a change in hand localization away from the rubber hand. ***p<0.001, **p<0.01, *p<0.05.*

The goal of **Study I** was to investigate the causal relationship between changes in perceived limb location and the subjective sense of body ownership. Some neurocognitive models of body ownership had suggested that recalibration of hand position sense towards the rubber hand was a pre-requisite for the illusion to develop (Botvinick & Cohen, 1998), whereas others placed emphasis on the visuo-tactile integration in peri-personal space which would in turn lead to a recalibration of hand position sense (Makin et al., 2008). To this end, we designed experimental conditions in which a change in perceived limb location could be induced without the participant noticing. We show that the illusion strength remains unaffected by relatively large changes in perceived hand location towards or away from the rubber hand (Fig. 8). These results indicate that the sense of body ownership of the rubber hand is not reliant on displaying a proprioceptive drift towards the rubber hand, and furthermore indicates that the proprioceptive drift should not be used as a proxy of the illusion by itself. However, these results also reproduce the previously reported difference between proprioceptive drift in the synchronous and asynchronous condition (the proprioceptive shift) for the static condition, indicating the rubber hand illusion and the proprioceptive drift are somehow correlated, albeit not at a causal level directed from proprioceptive drift to the subjective illusion. Our results do not rule out the possibility that the causal relationship is directed in the opposite direction, namely that sense of body ownership over the rubber hand induces changes in perceived hand location. This notion is compatible with existing neurocognitive models of body ownership (Makin et al., 2008), as well as recent computational models of body ownership based on Bayesian causal inference as outlined in the introduction (Samad et al., 2015).

4.2 STUDY II

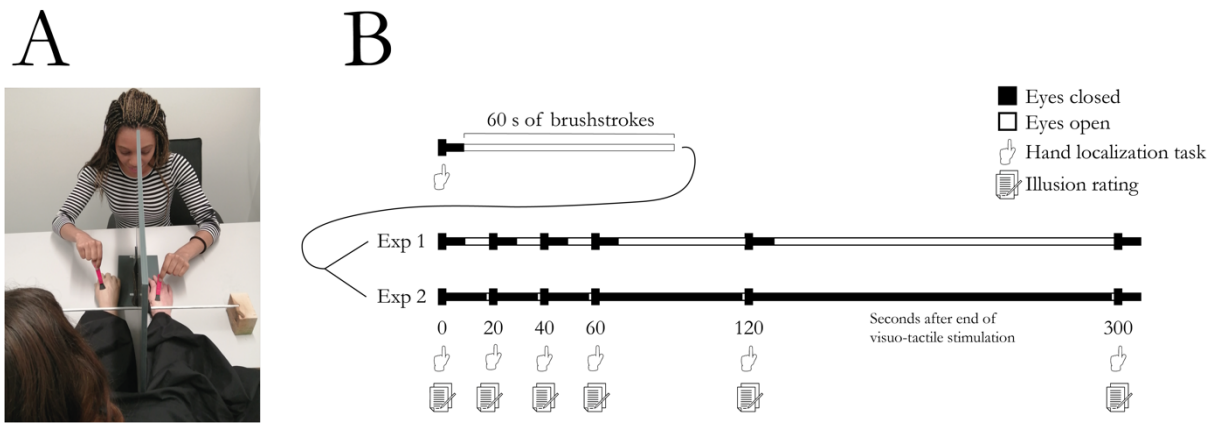


Figure 9. The main methods from Study II. ***A*** *depicts the experimenter inducing the rubber hand illusion on a subject by applying brush strokes to the participant's hand and the rubber hand. The metallic rod with the ruler marks used in the hand localization task for the proprioceptive drift is seen placed across the wrists of the participant's hand and the rubber hand but could easily be moved up to be placed across the fingertips right before the hand localization task.* ***B*** *is a schematic overview of the two experiments in Study II. The main difference between experiment 1 and 2 is the amount of time the participants had their eyes open and viewed the rubber hand.*

In **Study II**, we examined the persistence of the subjective illusion and the proprioceptive drift in the rubber hand illusion after the end of the visuo-tactile stimulation. In two experiments, we induce the classic rubber hand illusion for 60 seconds, and then stop the visuo-tactile stimulation. Subsequently, we measure the proprioceptive drift as well as subjective ratings of the illusions at several time points after the end of the visuo-tactile stimulation (Fig. 9). We show that both the proprioceptive drift and the subjective illusion persist for tens of seconds after the end of the visuo-tactile stimulation (Fig. 10, Panel A). Furthermore, we analyzed the slopes of the decay curves in the synchronous condition for both the subjective illusion and the proprioceptive drift which revealed strikingly similar decay curves (Fig. 10, Panel B). Finally, we show that the decay is unaffected by whether the participants have their eyes open, looking at the rubber hand or whether they have their eyes closed (comparison between experiment 1 & 2, Fig. 10, Panel C). Taken together our results indicate that the proprioceptive drift and the subjective illusion is highly correlated with regard to their decay after the end of the visuo-tactile stimulation, suggestive of a causal relationship between the two phenomena.

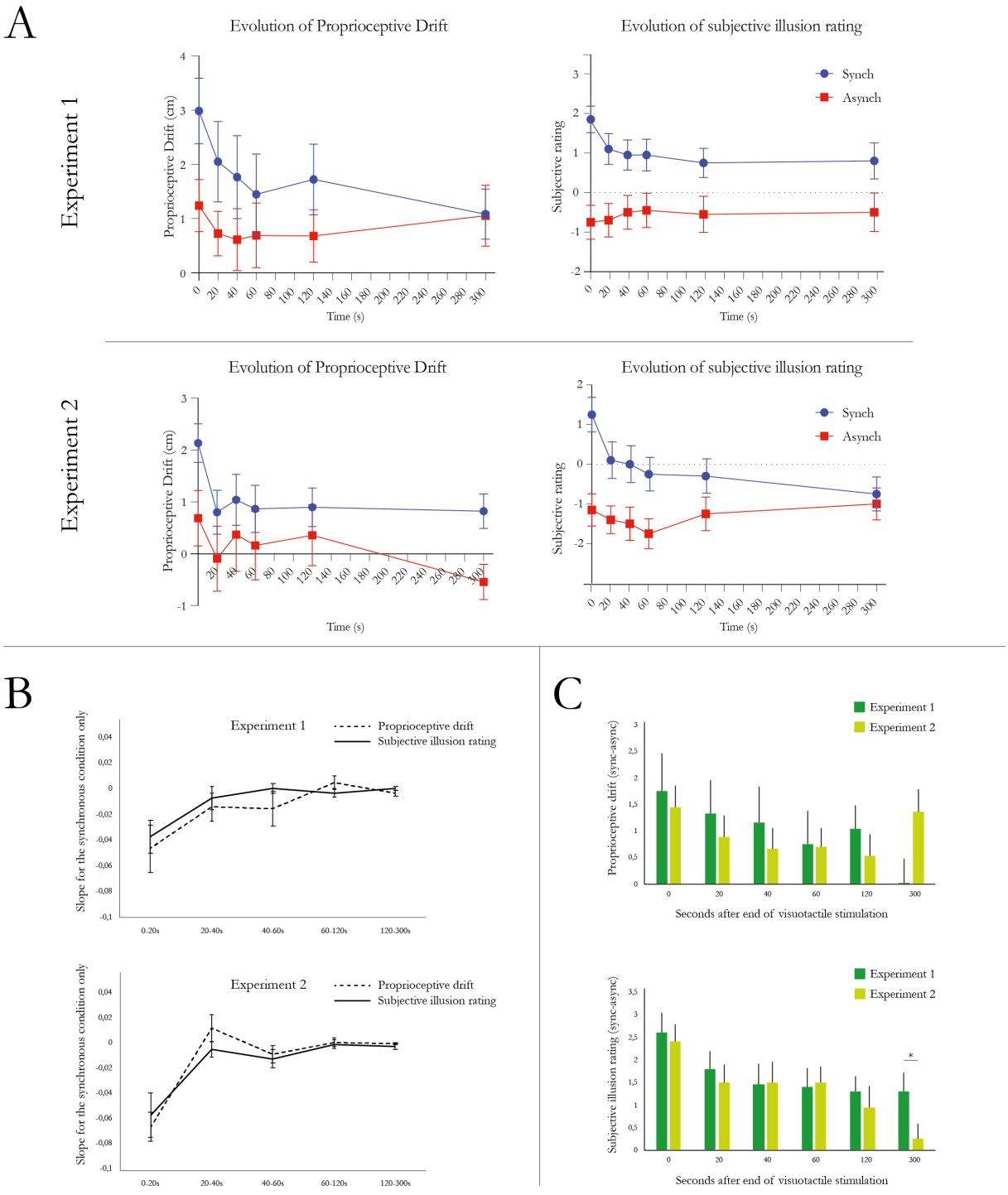


Figure 10. The main findings from Study II. ***A*** *depicts the rating of the ownership statement and proprioceptive drift in the synchronous and asynchronous condition in experiment 1 & 2. In* ***B,*** *the slopes for the curves of the synchronous condition was calculated for each time period between two measuring points in experiment 1 & 2. There were no differences between the slopes of the subjective illusion rating or the proprioceptive drift in neither of the experiments.* ***C*** *shows the interaction between synchrony and experiment (1 or 2). The analysis only showed a significant difference at the 300 second time point for the subjective illusion rating with higher ratings in experiment 1 compared to experiment 2. *p<0.05.*

4.3 STUDY III

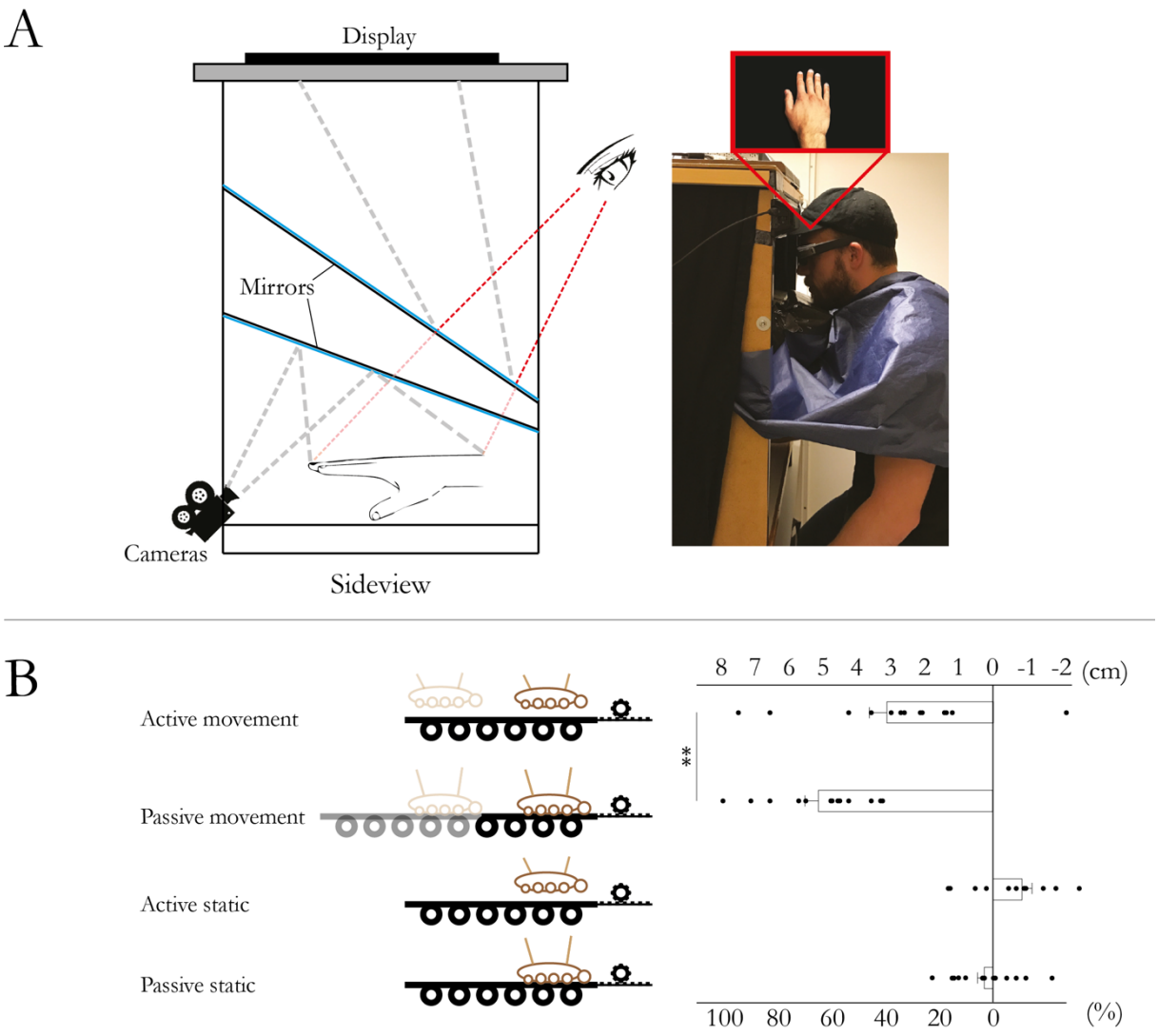


*Figure 11. The main methods and findings from Study III. **A** depicts the experimental setup. The participants hand was placed inside the hand illusion box. The participant viewed their hand from the first-person perspective inside the box. **B** The results showed that active unaware displacement of the participants hand caused a larger recalibration of hand position sense toward the visual position of the hand compared to passive unaware displacement. Note that the displacement of the participants hand was done without them noticing the displacement. 0 indicates the perceived position of the hand prior to the displacement, as well as the visual position of the hand throughout the trials. **p<0.01.*

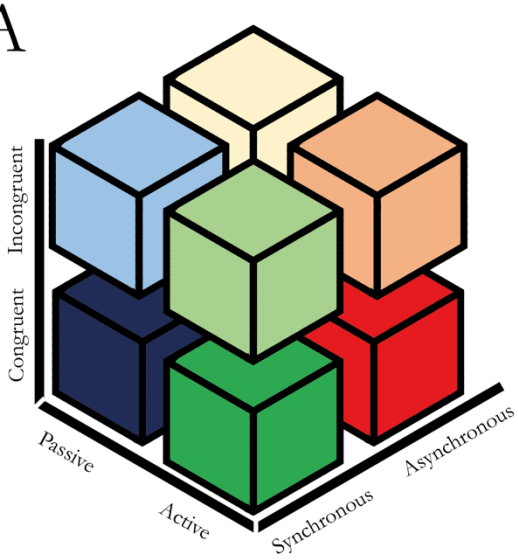
Study III aimed at comparing the visuo-proprioceptive adaptation during unconscious active and passive movements. We knew from the literature on prism adaptation and motor control that active movements lead to a faster and stronger recalibration of visual and proprioceptive maps (Beckett, 1980; Fernández-Ruiz et al., 2004; Hein & Held, 1958; Mikaelian & Held, 1964; Welch et al., 1979). However, it was unclear whether this recalibration is based on 1) conscious motor intentions or motor awareness and 2) salient error signals due to either sensorimotor or visuo-proprioceptive mismatches. In **Study I**, we had shown that participants

were surprisingly accurate in locating the position of their hand after it had been passively displaced without their awareness, and thus we were curious as to whether they would be less accurate if their hand had been displaced actively without their awareness. In **Study III**, we show that the same pattern of results is present with unconscious active and passive movements, where active displacement leads to a larger recalibration of perceived hand location towards the viewed position of the hand than passive displacement (Fig. 11). No such difference is seen in the static control conditions where there were no digital shift of the viewed hand and hence no displacement of the participant's hand, indicating that the recalibration cannot be attributed to general differences in the accuracy between the active and passive condition. We hence conclude that neither motor awareness, nor salient error signals is necessary for the increase in visuo-proprioceptive recalibration that is seen in active movements compared to passive movements, suggestive of an unconscious efference copy-based mechanism underlying the increased recalibration seen in the active conditions.

4.4 STUDY IV

In **Study IV**, we investigated the neural correlates of the sense of body ownership and agency, as well as their interaction. We employed a 2x2x2 factorial design to manipulate the sense of body ownership and agency independently (Fig. 12). Our results demonstrate that the sense of body ownership is associated with activity in the pre-central gyrus, the supra marginal gyrus and the cerebellum (Fig. 13). Our findings replicate previous studies that have identified frontal, parietal and cerebellar regions associated with the sense of body ownership (H Henrik Ehrsson et al., 2004; Gentile et al., 2013; Guterstam et al., 2013; Petkova et al., 2011). Interestingly, we also find a correlation between behavioral measures and parameter estimates for the activation in the precentral gyrus (PMd).

A



B

Condition	Acronym
Active/Synchronous/Congruent	ASC
Active/Aynchronous/Congruent	AAC
Passive/Synchronous/Congruent	PSC
Passive/Asynchronous/Congruent	PAC
Active/Synchronous/Incongruent	ASI
Active/Aynchronous/Incongruent	AAI
Passive/Synchronous/Incongruent	PAI
Passive/Asynchronous/Incongruent	PAI

*Figure 12. In **A**, a schematic illustration of the design matrix for the 2x2x2 design used in Study IV is shown. The conditions are color coded with the same colors used in the figures related to Study IV. In **B**, all the eight unique conditions as well as their acronyms and colors used in the figures related to Study IV are shown.*

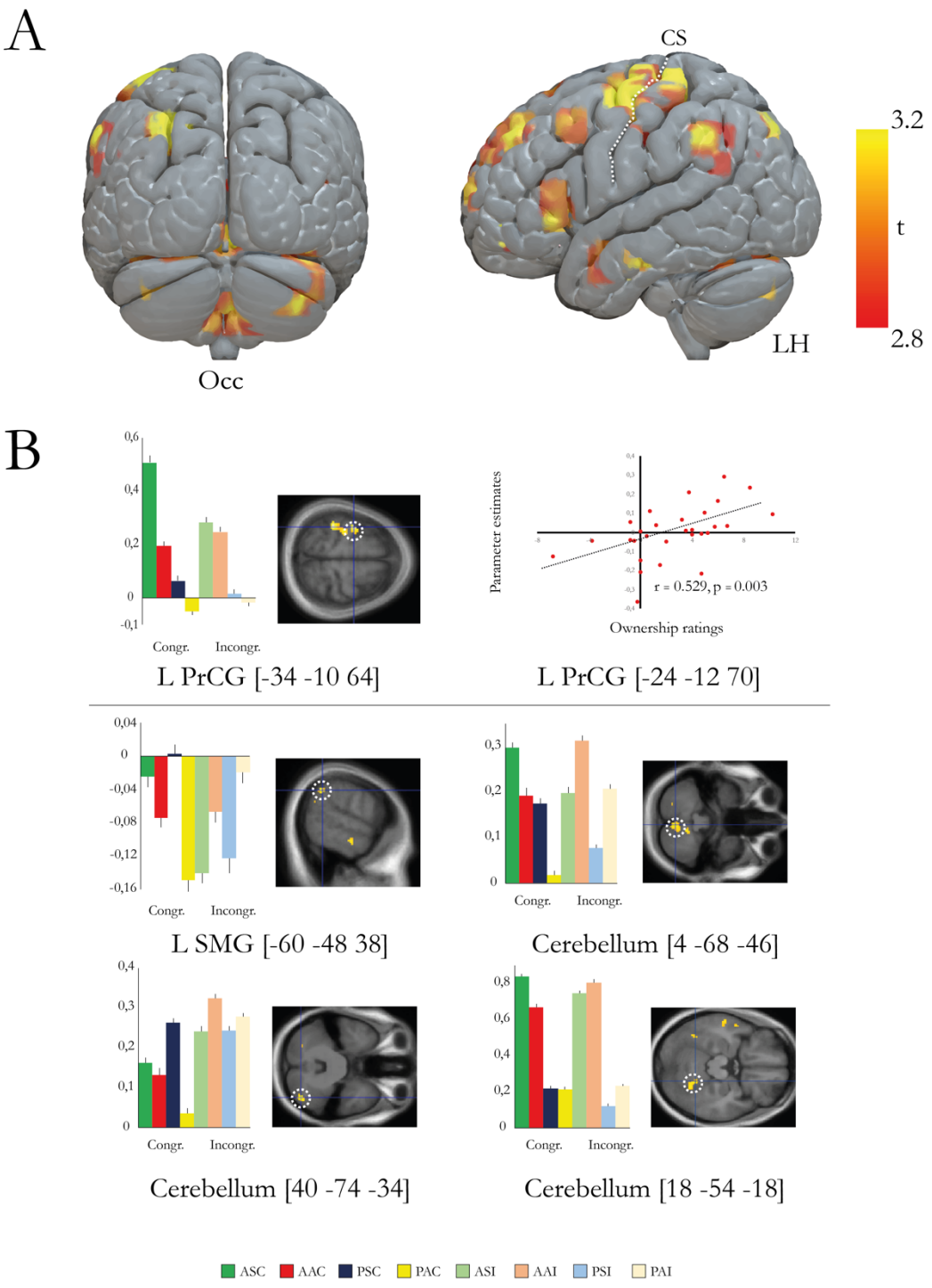


Figure 13. ***A.*** *Overview of the brain regions that display activation reflecting the sense of body ownership over the rubber hand. For display purposes only, the activations are projected on to a three-dimensional render of a standard brain with at a threshold of p<0.005 (uncorrected for multiple comparisons). LH, left hemisphere. Occ, occipital view. CS, central sulcus.* ***B.*** *Bar charts displaying the parameter estimates and SEs for the major peaks of activation, as well as one scatter plot of the correlation between parameter estimates and subjective illusion ratings for one activation peak in the pre-central gyrus (PMd). The coordinates are given in MNI space. The peaks are displayed in representative sections indicated by a dotted white circle on an activation map (p<0.005 uncorrected for multiple comparisons). L/R, left/right. PrCG, precentral gyrus. SMG, supramarginal gyrus.*

Furthermore, we identified the right superior temporal gyrus (STG), and the left PMd to be the brain regions that display activity associated with the sense of agency (Fig. 14). The PMd is anatomically connected to dorsolateral prefrontal cortex (DLPFC) and the PPC and is thus in an excellent position to integrate information regarding motor intentions from the DLPFC and information regarding the state of the body from the multisensory PPC.

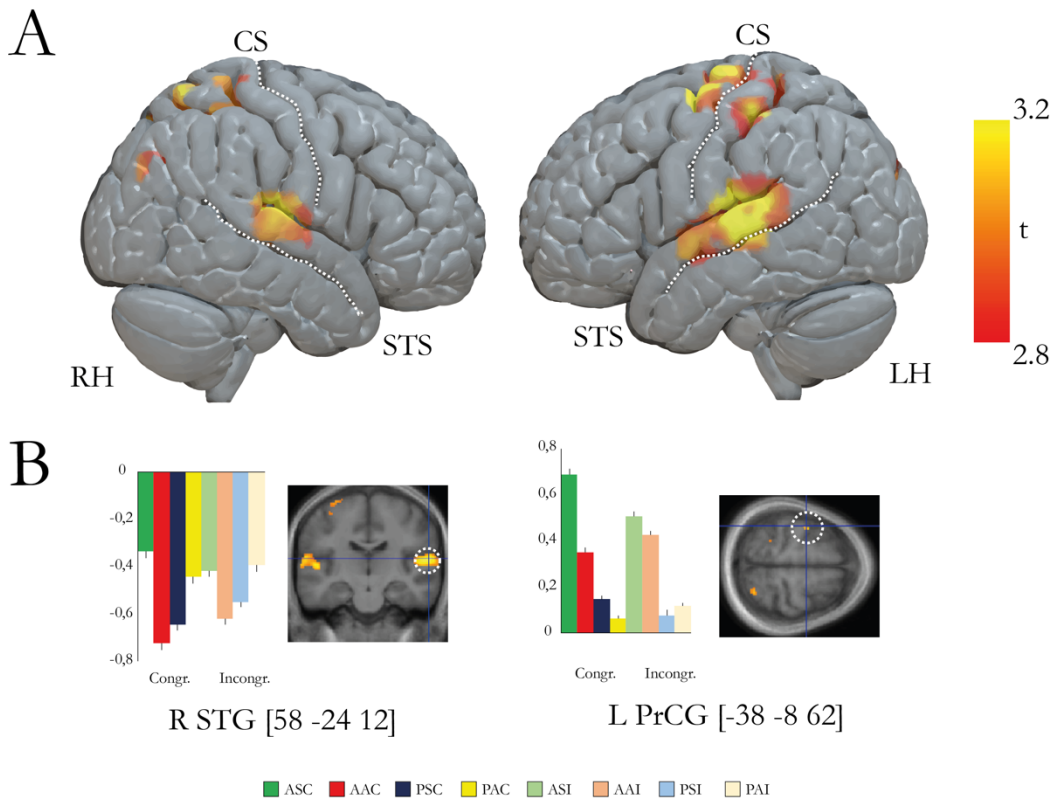


Figure 14. ***A.*** *Overview of the brain regions that display activation reflecting the sense of agency. For display purposes only, the activations are projected on to a three-dimensional render of a standard brain with at a threshold of p<0.005 (uncorrected for multiple comparisons). RH/LH, right/left hemisphere. STS, superior temporal sulcus. CS, central sulcus.* ***B.*** *Bar charts displaying the parameter estimates and SEs for the major peaks of activation. The coordinates are given in MNI space. The peaks are displayed in representative sections indicated by a dotted white circle on an activation map (p<0.005 uncorrected for multiple comparisons). L/R, left/right. STG, superior temporal gyrus. PrCG, precentral gyrus.*

We then analyzed the interaction between the sense of body ownership and the sense of agency. We conducted a within subjects, three-way interaction analysis including the factors synchrony (synchronous or asynchronous), movement type (active or passive) and congruency (congruent or incongruent). Our results show that the left post-central gyrus and left primary sensory cortex displays increased activation when experiencing agency over bodily objects compared to

external objects (Fig. 15). These areas have been implicated in a meta-analysis to be activated during self-attribution of the sense of agency (Sperduti et al., 2011).

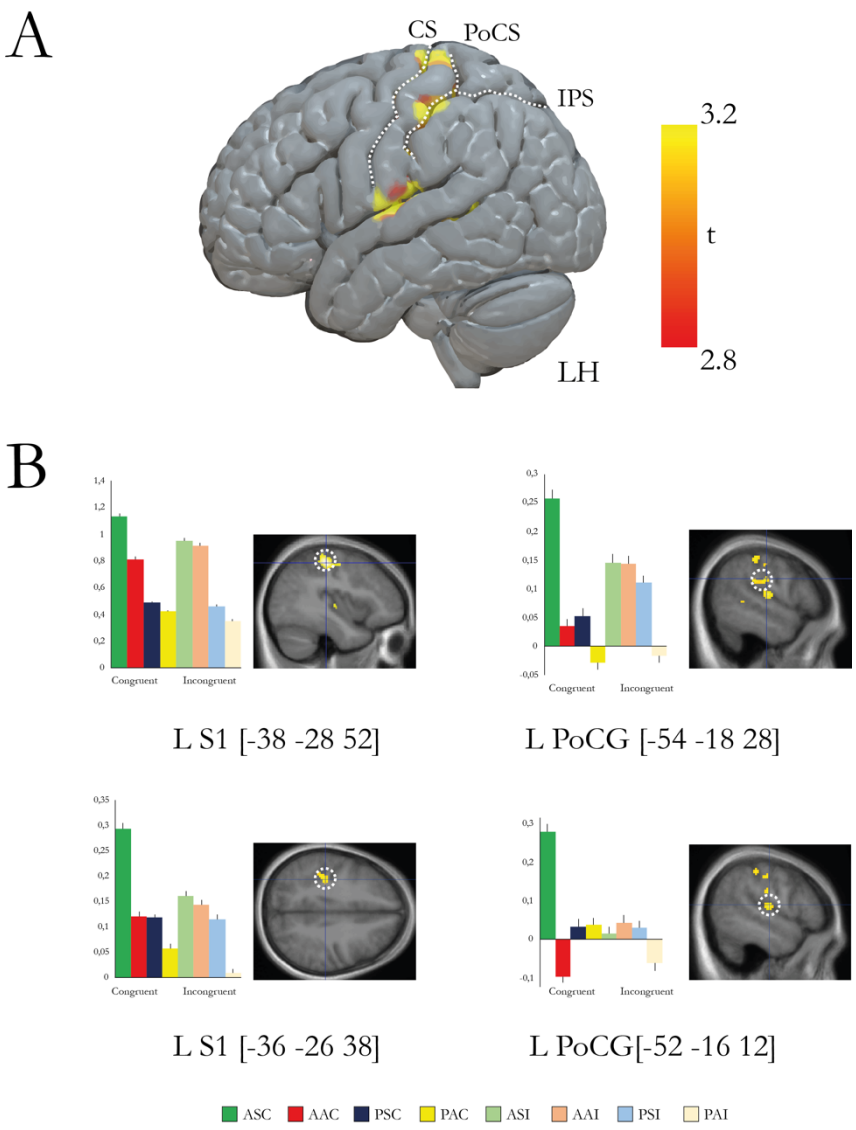


Figure 15. ***A.*** *Overview of the brain regions that display activation reflecting increased activation related to agency of bodily objects compared to external objects. For display purposes only, the activations are projected on to a three-dimensional render of a standard brain with at a threshold of p<0.005 (uncorrected for multiple comparisons). RH/LH, right/left hemisphere. IPS, intraparietal sulcus. PoCS, post-central sulcus. CS, central sulcus* ***B.*** *Bar charts displaying the parameter estimates and SEs for the major peaks of activation. The coordinates are given in MNI space. The peaks are displayed in representative sections indicated by a dotted white circle on an activation map (p<0.005 uncorrected for multiple comparisons). L/R, left/right. PoCG, post-central gyrus. * indicates activation peaks that do not survive the small volume correction.*

To analyze which brain regions that display increased activity during experience of agency over external objects compared to bodily objects, we defined a contrast that was the inverse of

the three-way interaction for bodily agency. The analysis revealed that the left visual association cortex was more active during the experience of agency of external objects compared to the experience of agency of bodily objects (Fig. 16).

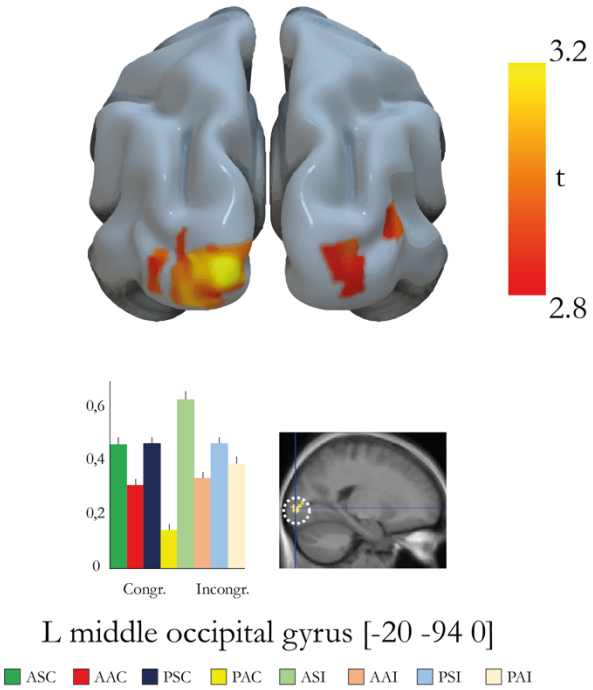


Figure 16. The brain regions that display increased activity associated with agency of external objects compared to agency of bodily objects defined as a contrast that was the inverse of the three-way interaction used in figure 15. The results show activation in the left medial occipital gyrus. The coordinates are given in MNI space. The peak is displayed in a representative section and indicated by a dotted white circle on an activation map ($p<0.005$ uncorrected for multiple comparisons).

5 DISCUSSION

This thesis aimed at investigating the perceptual and neural mechanisms of body ownership, in particular its relation to voluntary action and processes underpinning the sense of agency. We use different bodily illusions and sensorimotor illusions to manipulate certain aspects of the sense of body ownership, agency or voluntary action in a precise and predictable way. The experiments in this thesis characterized the perceptual and neural mechanism of these manipulations of body ownership and agency and show that the results are consistent with multisensory and motor-sensory computational models of these phenomena, respectively. In **Study I** we challenge the notion that a change in hand position sense towards the rubber hand is a prerequisite for the experience of ownership of the rubber hand. We show that the subjective experience of ownership is unaffected by mechanically induced changes in hand position sense, even when directed away from the rubber hand. In **Study II**, we characterize the temporal relationship between the subjective experience of ownership and the visuo-proprioceptive recalibration of hand position sense, in particular we show that the subjective experience of ownership as well as the recalibration of hand position persist for tens of seconds after the end of the visuo-tactile stimulation. Furthermore, the temporal dynamics of the decay of these two measures are strikingly similar. In **Study III**, we investigate the visuo-proprioceptive recalibration of hand position sense in relation to voluntary action. In particular, we investigate whether visuo-proprioceptive recalibration of hand position sense is affected by unconscious voluntary action. We show that unconscious active movements lead to greater recalibration compared to unconscious passive movements. In **Study IV**, we examine the neural correlates of the sense of body ownership and agency, and the interaction between these two experiences. We show that the sense of body ownership and the sense of agency can be behaviorally dissociated, and furthermore, we show that they have distinct neural correlates, consistent with the notion of them being two separate processes.

5.1 THE SENSE OF BODY OWNERSHIP – INFERRING AND INTEGRATING

How is the sense of body ownership brought about, and what governs the visuo-proprioceptive recalibration seen the rubber hand illusion? Our results from **Study I** and **Study II** demonstrate two things: first of all, in **Study I** we show that the subjective experience of body ownership can happen independent of the recalibration of hand position sense towards the rubber hand. This result is consistent with the recent causal inference model of body ownership which states that an inference to a common cause happens first, followed by an integration the multisensory signals (Samad et al., 2015). Such a notion makes teleological sense, otherwise we would be recalibrating our visuo-proprioceptive system to the sight of other people's limbs over which

we do not experience any sense of body ownership. Second, in **Study II** we show that once a sense of body ownership and visuo-proprioceptive recalibration of hand position has been established in the rubber hand illusion, they persist for tens of seconds after the end of the visuo-tactile stimulation and seem to display striking similarities with regards to the speed and dynamics of their decay, suggestive of a causal relationship between the two phenomena. To interpret the results from **Study II** within the same causal inference framework requires some adaptation of the model since the causal inference model only has been empirically validated for the integration of multisensory stimuli, while in **Study II**, we investigate the segregation of multisensory stimuli. Applying the same model, somewhat speculatively, one could assume that during the illusion, the prior probability that the rubber hand is one's own has been updated after the inference to a common cause has been made. Once the visuo-tactile stimulation stops, the now integrated stimuli will start to be segregated, and the inference to a common cause transforms to inference to separate causes. However, with this model, one might rightfully ask why there is a segregation at all, could the illusion not be maintained indefinitely as long as no new contradicting sensory information is presented? One could speculate that the spontaneous decay of the illusion and the proprioceptive drift happens due to either or a combination of (i) the possibility that the prior probability indicating that the rubber hand is one's own hand is weaker than the "native" prior of the rubber hand not being one's own hand, which might require constant sensory information in support of its maintenance or (ii) the small visuo-proprioceptive mismatch might gradually, over time build up sensory information in opposition of the unified inference, ultimately leading to its segregation. However, the precise causal and temporal between the subjective experience of body ownership and the recalibration of hand position sense needs to be studied further in detail, in particular their relationship during the induction of the illusion.

In **Study IV**, we show that the sense of body ownership is associated with activity in know multisensory areas in frontal, parietal and cerebellar regions. It is worth noting that the peaks we observe in our experiment are not completely overlapping with the peaks found in previous papers (H Henrik Ehrsson et al., 2004; Gentile et al., 2013, 2015; Guterstam et al., 2013). We interpret this slight difference to be due to the differences in the level of motor activity and the type of multisensory integration between the types of bodily illusions. In the moving rubber hand illusion, as opposed to the classic rubber hand illusion induced by synchronous brushstrokes, the participants perform active movements, and the synchronous multisensory signals to be integrated are mainly visuo-kinesthetic (i.e., proprioceptive signals from the finger flexing and visual signals from the moving rubber hand's finger, although tactile stimuli from the skin covering the joints is also present). These differences could lead to differences in the

exact localization of the activation peaks, and for this reason, we performed the localizer experiments described in the methods to identify the exact activation peaks within the regions of interest in our experiment. Of particular interest is the activity in the PMd, which we show to correlate with subjective measures of ownership, replicating the findings from previous body illusion studies which have found similar correlations in the PMv (H Henrik Ehrsson et al., 2004; Guterstam et al., 2013). Apart from the known multisensory neuronal populations in the premotor cortex (Fogassi et al., 1996; M. S. Graziano et al., 1997; M. S. A. Graziano & Gross, 1998), and the fact that it has strong anatomical connections to other multisensory areas in the parietal lobe as well as to the primary motor cortex (Dum et al., 2002; Porter & Lemon, 1995), the premotor cortex has in a recent body illusion study on macaques been shown to integrate multisensory stimuli in a Bayes-optimal way (Fang et al., 2019), further implicating its role in the multisensory mechanisms involved in generating a sense of body ownership. Taken together, one could theoretically speculate that the bodily representation is grounded in a parieto-frontal network, where the premotor cortex infers whether the sensory signals from multisensory parietal regions share a common cause, which in turn updates the priors of these multisensory signals thus designating the degree of integration.

In light of these findings, one might speculate what the potential benefits of having a system dedicated to assigning ownership of bodies and limbs are? This system, which is highly efficient at identifying and self-attributing body parts to one's self has been proposed to have evolved from the more basic need to segregate one's own body from the outside world (Frédérique de Vignemont, 2015; Guterstam, 2016). The multisensory integration within peri-personal space leading to the ability to distinguish bodily from non-bodily objects was likely accompanied by the advantage of being able to protect one's body from physical harm more efficiently (Dijkerman & Farnè, 2015), a notion that is also consistent with other reductionistic ideas that grounds the sense of body ownership in an affective experience of one's own body (Frédérique de Vignemont, 2015). Such theories have been proposed in both the philosophical and neuroscientific literature (Frédérique de Vignemont, 2015; Guterstam, 2016), and has been particularly outlined in the bodyguard hypothesis of the sense of ownership (F de Vignemont, 2017). It is interesting to speculate on the ubiquity of such a system, since much of the knowledge of the multisensory mechanisms comes from electrophysiological studies on non-human primates, indicating that they possess the necessary infrastructure for such a system. However, since they cannot explicitly communicate their subjective experiences it is difficult to infer whether the neuronal activity is also accompanied by any subjective experiences of ownership. With that said, recent studies employing different proxy measures of the sense of body ownership have demonstrated some kind of bodily illusion in non-human primates (Fang

et al., 2019; Shokur et al., 2013) as well as rats (Wada et al., 2016), indicating that at least some of the processes underlying the bodily illusion seem to be conserved across species.

5.2 THE SENSE OF AGENCY – PREDICTING AND COMPARING

As outlined in the introduction, the sense of agency has been reported to consist of different components with different temporal relationship to the action and subsequent sensory feedback. The prospective component of agency is thought to arise prior to the effect of the action has been registered, whereas the retrospective component of agency arises after the action and its sensory effects have been registered. Converging evidence support the notion that retrospective comparisons between sensory predictions and reafferent signals is the dominant process through which a subjective sense of agency is elicited (David et al., 2008; Haggard, 2017; Synofzik et al., 2008). However, the judgement of agency also seems to be influenced by a prospective component of agency, which has been shown to be related to the causal contingencies of the action and outcome, with a higher impact of the prospective component on the sense of agency seen in conditions with high causal contingencies (A. Sato, 2009). These results fit well with a recent Bayesian framework that applies weights to the various sources of information (i.e., priors and sensory signals) based on their relative reliability (Legaspi & Toyoizumi, 2019; Wolpe et al., 2013; Lau et al., 2007). This would mean that when predictability of the sensory consequences of an action is high, the actual sensory feedback receives a lower weighting than when the predictability is low. This has been shown for the implicit intentional binding measure as well as explicit judgements of the sense of agency; if the reliability of the sensory feedback is reduced by the introduction of noise, there's less shift in the perceived action timing towards the feedback (Wolpe et al., 2013), and furthermore, if the predictability of an outcome is high, there is a larger shift in perceived action timing towards the feedback, and participants also report a higher sense of subjective agency (A. Sato, 2009).

In this thesis, I propose that this distinction between the prospective components of agency and the retrospective components of agency is relevant for agency in a bodily context. I base this proposition on the empirical evidence suggesting that the prospective components are dependent on the predictability of actions, i.e., the causal contingencies, whereas the retrospective component is dependent on a post-hoc comparison between intended and actual sensory feedback. Since the physical body is an object through which we've interact with the world our whole lives, the a priori causal contingencies are high, and thus the predictability of the action outcomes is high, meaning that the prospective predictions can be weighted higher

in the process of agency attribution. Whereas for the sense of agency of external objects and events, new causal contingencies need to be collected and validated, and hence, the sense of agency will (at least initially) be more dependent upon a retrospective matching between predicted and actual sensory feedback. Until recently, separating the bodily related sensory feedback of an action from the external sensory feedback was difficult since all actions will generate some kind of sensory feedback from the body. However, by using the moving rubber hand illusion, the sense of body ownership and agency can be transferred onto the rubber hand, and furthermore, this can be manipulated. By placing the hand in an anatomically congruent position while the participants control the rubber hand actively will induce a sense of ownership as well as a sense of agency, and hence the sensory feedback from the participants hand as well as the rubber hand will both be mapped onto the same body part, which is perceived as one's own. By rotating the rubber hand 180 degrees, the rubber hand and the participant's hand will be perceived as two separate objects, and hence, the sensory feedback from the rubber hand and from the participant's hand will be segregated, in essence leading to the visual feedback from the rubber hand being segregated from the tactile and proprioceptive feedback from the participants hand (Fig. 17, right panel). This will lead to the proprioceptive and tactile (kinesthetic) signals to be highly predictable since they are interpreted arising from the own body, whilst the visual signals are less predictable and thus the actual visual sensory feedback receives a higher weighting (Fig. 17, right panel). This dissociation is the basis for the comparison between agency of bodily objects and non-bodily objects and events. I propose that agency of bodily objects is more reliant on the prospective, causality dependent component of agency, while agency of external objects is more reliant on retrospective comparison of the actual sensory feedback and the predicted sensory feedback. The neuroimaging results from **Study IV** implicates the primary somatosensory area to be the brain region related to the bodily agency, likely representing the predictions regarding sensory feedback from the own body (Shergill et al., 2014). Conversely, we show that agency of external objects is associated with increased activity in visual areas, consistent with the proposed model (Fig. 17). Further analyses of **Study IV** should investigate whether there is any increase in effective connectivity between the left PMd (which was associated with the sense of agency regardless of whether it was of bodily or external objects) and primary sensory cortex or visual association cortex for the different types of agency.

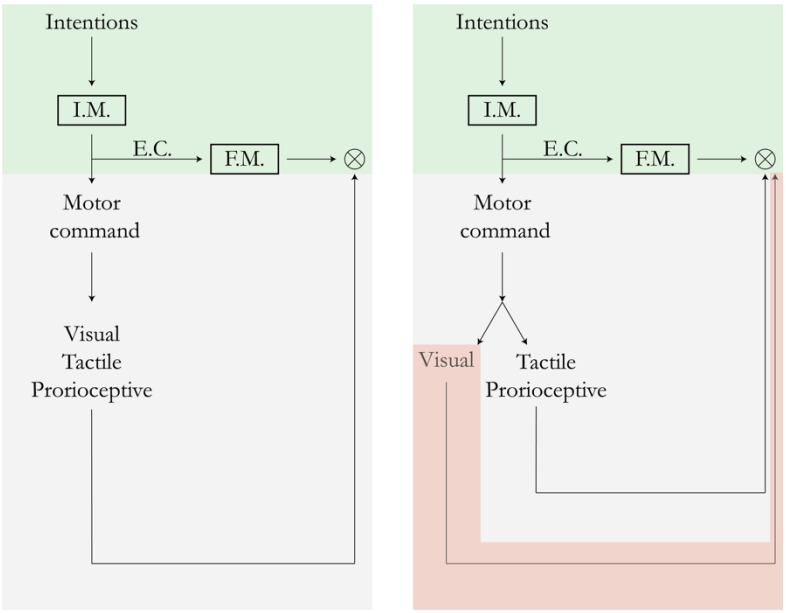


Figure 17. In the left panel, agency of bodily objects is illustrated. The visual, tactile and proprioceptive signals are all interpreted as arising from the own body, and hence they are highly predicted by the forward model (F.M.). The right panel shows the sense of agency of non-bodily objects. The visual feedback is now segregated from the tactile and proprioceptive, and hence is not predicted to the same extent since it is not perceived as arising from the own body. The weighting is thus more reliant on the retrospective component, due to the lower predictability of the visual feedback. The green field represents the processes that happen before the action, and thus represent the prospective component of agency, whereas the grey field indicate the processes after action execution, thus representing the retrospective component of agency. The "priors" in the causal inference model of agency is thus contained within the green field, since they represent the prospective components of agency.

One might wonder why the brain would possess two separate mechanisms for attributing agency. I do not think the prospective component of agency is specific for agency of bodily actions, rather I think there are general advantages of having two mechanisms that can be applied to all actions and outcomes. As described in the proposed Bayesian model of agency, the attribution of agency depends on a joint weighting of the prior probability as well as the sensory feedback. Having a system that depends on both the priors and the post-hoc sensory feedback means that the system is dually protected against being limited in situations of uncertain or noisy sensory feedback, for instance, when moving our limbs in the dark without visual feedback, we can still experience a sense of agency over our actions. At the same time, being able to rely more heavily on the sensory feedback in cases of weak priors makes us learn new causal associations to our actions and thus over time build causal structures that underlie future predictions. Alone, neither the prospective component nor the retrospective component seems to be sufficient, only relying on the predictions of the prospective component can lead to gross miscalculations (since the predictions can be faulty), whereas only relying on the retrospective component seem to run the risk of misclassifying events as self-caused when they

are not, which has been proposed to be the case for schizophrenic patients (S. J. Blakemore et al., 2000; Shergill et al., 2005, 2014).

Furthermore, it is also interesting to consider the potential benefits of having a sense of agency at all. I speculate that the sense of agency developed from a more basic sensory filtration system, aimed at being able to distinguish self-generated sensory signals from externally generated sensory signals by modulating the saliency of the afferent signals (Crapse & Sommer, 2008; Kilteni et al., 2019; Maimon et al., 2010; Polack et al., 2013; J. F. A. Poulet & Hedwig, 2006; Schneider et al., 2014; Shergill et al., 2003). Such a system is relevant not only for the protection of one's body from physical harm, by for instance increasing the saliency of a predator's sound, but also for communication and social interactions within populations. Interestingly, various sensory modulatory effects based on the principle of corollary discharge (equivalent to the efference copy) have been observed in across the animal kingdom (Crapse & Sommer, 2008). One of the most striking examples can be found in crickets, where self-generated chirps are accompanied by an inhibition of auditory neurons, indicating that it is a preserved basic mechanism for sensory predictions (J. f. a. Poulet & Hedwig, 2003). Once such a system was in place and able to distinguish self from externally generated sensory signals, it could have been adopted to also infer a sense of agency according to the neural recycling hypothesis (Dehaene & Cohen, 2007). The benefits of not only predicting and suppressing the self-generated reafferent sensory signals, but also self-attributing the causality of the generated sensory signals to one's self is that it could lead to improvements of the predictions. Without such self-attributing, faulty predictions would lead to just repeatedly interpreting the sensory signals as external. Interestingly, speculating in such a neural recycling hypothesis predicts a prospective component to the sense of agency, since the sensory filtration mechanisms need to be deployed prior to receiving the sensory feedback, one piece of the puzzle which was missing from the comparator model.

5.3 OWNERSHIP AND AGENCY – PROTECTING AND GUIDING

In line with my proposition above, I do not propose that there is anything special regarding the sense of agency of bodily objects aside from their inherent familiarity and the high predictability of the reafferent sensory signals that bodily actions produce. One interesting prediction that can be derived from this notion is that given the same amount of training, non-bodily objects should enjoy the same amount of predictability and hence, display the same pattern of results. This is a testable hypothesis, wherein participants could for instance receive a tool or some other manipulandum to use frequently enough for their forward models to

become more precise and efficient at predicting the sensory outcomes. This could be compared to the use of tools that have not been trained to the same extent. Recent studies on tool use have shown that the recalibration of peri-personal space around the hand can happen after a relatively short period of tool use (Canzoneri et al., 2013; Farnè & Làdavas, 2000; Guterstam et al., 2018; Holmes, 2012; Holmes et al., 2007), indicating that there is a plasticity in the system that can cater to such recalibrations.

In the recently proposed Bayesian causal inference model for the sense of agency, the authors propose that a sense of agency can arise for unintended actions if the sensory signals are reliable enough (Legaspi & Toyoizumi, 2019). The authors do not discuss whether the opposite is possible, i.e., given strong enough priors, would it be possible to experience a sense of agency without any sensory feedback? The predictions regarding the macroscopic movements of our bodies are likely the most robust, and hence would it be possible to experience a sense of agency of one's body without any movement or sensory feedback? Anecdotally, subjective reports from participants experiencing the classical (afferent) rubber hand illusion indicated that they perceived that if they were to move their finger, the rubber hand would move in the same manner, but once they performed the movement and noticed that the rubber hand remained static, the illusion broke down. Similarly, when looking at our hands, we can experience an implicit sense that if we were to decide to move the hand, the hand would comply. These sensations cannot be attributed to a retrospective comparison between predicted and reafferent sensory signals, and thus has to be attributed to a prospective component of agency. Such prospective accounts of agency judgements have yet to be investigated, and the questionnaires used in the body illusion studies on the sense of agency generally fail at capturing this sensation since they are usually anchored to the performance of an action.

Finally, one might ask to what goal the sense of ownership and the sense of agency collaborate? I propose that the most likely advantage of both processes is the protection of the physical body from harm and the improvement of goal-directed movements. In essence, both the sense of body ownership and the sense of agency has the ability to separate one's self from the environment, with regards to what belongs to one's self and to what was caused by one's self, respectively. The self-attribution of the physical body leads to better sensory predictions and the self-attribution of actions leads to fine-tuning of the forward models which gives rise to more efficient actions. In **Study IV** of this thesis, the PMd was identified as the brain region that is activated in both these processes, the self-attribution of limbs and the self-attribution of actions. One could thus hypothesize that the sense of owning a body and the sense of controlling it both converge on to PMd, which with its dense anatomical connections to the

primary motor cortex serves as an excellent candidate to guide goal directed actions (Dum et al., 2002; Porter & Lemon, 1995).

5.4 RELEVANCE FOR CLINICAL POPULATIONS

This thesis investigated the behavioral and neural correlates of the sense of body ownership and agency with results that are relevant for research in both clinical and applied neuroscience. In particular, the findings from the **Studies I-IV** are relevant for research on neuroprosthetics, where the development of prosthetics that the patients both experience a sense of ownership and agency over would vastly improve the quality of life for those patients. Previous research has shown that amputees can experience a sense of ownership of robotic hands when receiving synchronous visuo-tactile stimulation from the robotic hand and their real hand (H Henrik Ehrsson et al., 2008; Rosén et al., 2009). Furthermore, controlling a robotic hand with electromyographically (EMG) measured muscular activity has been shown to induce a sense of agency of the robotic hand (Marasco et al., 2018; Y. Sato et al., 2018). However, these studies all employed peripheral somatosensory stimulation or muscular activity as the means to generate the sense of ownership and/or agency, an approach that is not always possible and still requires continuous stimulation for the maintenance of the illusory experiences. Until recently, it was unclear whether direct electrical stimulation of the cortex could be integrated with other sensory modalities to produce the sense of body ownership in a body illusion setup. In a recent study, Collins and colleagues showed that electrical stimulation of the primary sensory cortex combined with visual stimuli of a rubber hand in the rubber hand illusion could generate a sense of ownership of the rubber hand (Collins et al., 2017). This finding paves the way for future brain-computer interfaces that directly stimulate the brain regions involved in producing these sensory experiences, hopefully leading to improved prosthetics that feel like real limbs. To this end, the studies in this thesis which characterized some of the perceptual processes and neural correlates of the sense of ownership and agency can provide valuable insights; in **Study IV**, we elucidate the neuroanatomical correlates of the sense of body ownership and agency as well as their interaction, which can serve as future target regions for these kind of interventions. Furthermore, in **Study II**, we show that the sense of ownership as well as the recalibration of hand position sense that underlies the proprioceptive drift is maintained for tens of seconds after the end of the visuotactile stimulation, indicating that constant stimulation is not necessary, which has been one of the major hurdles to overcome with developing neuroprosthetics with a sense of ownership.

Moreover, accumulating evidence suggest that schizophrenic patients have impairments in predicting the sensory consequences of their actions. Hence, they rely more on the retrospective component of agency i.e., they are more likely to causally link two events to each other based on the physical relation between action and outcome, so-called altered perceived causality (Wende et al., 2015). Since the proposed mechanism for these impairments is the inadequate ability to generate sensory predictions of their own actions (S. J. Blakemore et al., 2000; Chris D Frith et al., 2000; Shergill et al., 2005), the results from the studies in this thesis, in particular **Study IV** which sheds light on the neural mechanisms of the sense of agency, might be relevant for future diagnostic and therapeutic tools for patients suffering from this debilitating illness. Unfortunately outside the scope of this thesis, future experiments should elucidate whether schizophrenics display the same neural activation pattern associated with the sense of body ownership and agency as well as their interaction.

In conclusion, the studies in this thesis expand our knowledge of two fundamental processes of bodily awareness: the process of self-attribution of our limbs (body ownership) and the process of self-attribution of actions (agency). Together, the results from **Studies I-IV** provide evidence in favor of the sense of body ownership being dependent on multisensory mechanisms while the sense of agency is dependent on the prediction and comparison of reafferent sensory signals. Furthermore, the results from **Study IV** indicate that these two processes are perceptually and neurally distinct, with a possible integrative component with regards to the physical body. Increasing our understanding of these processes and their underlying neural mechanisms has implications for both the cognitive neuroscientific odyssey of understanding self-consciousness as well as for clinical research on patients with disturbances in these processes.

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